On cosmine: its origins, biology and implications for sarcopterygian interrelationships

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Received: 28 Nov. 2017
Accepted: 31 Jan. 2018
Editor: O. Otero

Key words
Cosmine
Dermal skeleton
Devonian
Paleohistology
Sarcopterygians
Scales

Abstract. – Cosmine is a combination of tissues (enamel, dentine, and bone) and a structure (pore-canal system) not found in living vertebrates. Long considered a synapomorphy of sarcopterygians (lobe-finned fishes), new discoveries and phylogenetic interpretations have shown that the assembly of cosmine is a deeper evolutionary event than previously thought and that cosmine constitutes a primitive feature of osteichthyans (bony fishes). A precursor of both cosmine and ganoine might have been present in the last common ancestor of sarcopterygians and actinopterygians (ray-finned fishes). However, despite numerous and thorough studies on cosmine since the late 19th century, its role and biological properties are still a mystery. Currently, the most consensual hypothesis considers cosmine as a metabolic regulator of mineral ions through intricated processes of deposition and resorption of dermal tissues. A new ontogenetic and phylogenetic scenario is emerging from microtomographic data revealing that a pore-canal system initially associated with multiple superimposed odontodes in stem osteichthyans and early sarcopterygians was reorganized and simplified in rhipidistians into a uniform cosmine sheet with a single layer of enamel overlying the dentine (eucosmine). In this review, I will summarize the current knowledge of cosmine origins, structure, development, and possible function based on previous research. I will also present new histological data on poorly known early sarcopterygians to highlight the importance of histological studies for upcoming analyses of sarcopterygian interrelationships. Future efforts to unravel the evolution of cosmine will need new virtual and three-dimensional approaches to paleohistology that will change our current framework of studying early vertebrate evolution and certainly revolutionize our understanding of this distinctive feature.

Résumé. – La cosmine : origines, biologie et implications phylogénétiques chez les sarcoptérygiens.

La cosmine est une combinaison de tissus (émail, dentine et os) et de structure (un système de pores et de canaux) sans équivalent parmi les vertébrés actuels. Longtemps considérée comme une synapomorphie des sarcoptérygiens (poissons à nageoires charnues), de nouvelles découvertes et interprétations phylogénétiques ont montré que la mise en place de la cosmine est un phénomène évolutif plus ancien que l'on ne croyait et qui constitue une caractéristique commune et primitive pour l'ensemble des ostéichtyens (poissons osseux). Les précurseurs de la cosmine et de la ganoine seraient déjà présents chez l'ancêtre commun des sarcoptérygiens et des actinoptérygiens (poisons à nageoires rayonnées). Cependant, malgré de nombreuses études paléoichtyologiques depuis la fin du XIXe siècle, le rôle et les propriétés biologiques de la cosmine demeurent un mystère. L'hypothèse la plus consensuelle donne à la cosmine un rôle métabolique dans la gestion des ions minéraux à travers le dépôt et la résorption des tissus dermiques la constituant. L'avènement des techniques de microtomographie et de modélisation virtuelle en 3D permettent désormais de commencer à proposer un scénario ontogénétique et phylogénétique de la formation et l'évolution de la cosmine chez les ostéichtyens, depuis un stade primitif où de nombreux odontodes superposés s'associaient à un système de pores et de canaux chez les premiers ostéichtyens, vers une cosmine plus uniforme formée par une seule couche d'émail recouvrant la dentine (eucosmine) chez les sarcoptérygiens rhipidistiens. Dans cet article de révision, je résumerai l'ensemble des connaissances actuelles sur les origines, la structure, le développement et les possibles fonctions de la cosmine tirées des études passées. Je présenterai également de nouvelles données histologiques de certains sarcoptérygiens anciens méconnus afin de mettre en évidence l'importance des études histologiques pour les futurs travaux s'intéressant à la phylogénie des sarcoptérygiens. Désormais, toute étude s'attaquant à l'origine évolutive de la cosmine nécessitera des nouvelles approches de reconstruction virtuelles, qui sont amenées à révolutionner notre cadre d'étude sur les vertébrés anciens, afin de percer les mystères de cette structure singulière.

Cosmine is one of the most puzzling histological features of early vertebrates. The term "kosmine" was introduced by Williamson (1849) to describe the vascular dentine layer of the scales of *Lepidotes* and 'palaeoniscoid' actinopterygians (ray-finned fishes) and early sarcopterygians (lobe-finned fishes), as opposed to dentine as present in the teeth. Later, Goodrich (1907) restricted the "cosmine" to the scales of sarcopterygians and he used it to characterize the dentine present in the newly coined term "cosmoid scale" of sarcopterygians when associated with a thin enamel layer and a pore-canal system pervading the dentine. The studies of Gross (1956) and Ørvig (1969a) established the current definition of the so-called "true" cosmine (eucosmine) as a combination of dermal tissues composed of a single layer of enamel and dentine incorporating a well-developed pore-canal system overlying a vascular bone layer (Sire *et al.*,

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Table I. – Definitions of the main terms used throughout this review to describe the tissues and structures related to cosmine in osteichthyans. Terminology and homologies mainly after Gross, 1956; Janvier, 1996; Sire *et al.*, 2009; Schultze, 2015; Qu *et al.*, 2016.

Enamel	*Enamel* is a highly mineralized, prismatic, avascular and acellular dermal product found in the outer layer of the teeth, dermal bones, scales, and fin rays of vertebrates. *Enamel* is unique in being the only non-collagenous mineralized vertebrate skeletal component, both odontogenic and skeletogenic. *Enamel* formation (amelogenesis) consists of two phases: deposition of an organic matrix by ameloblasts and its subsequent mineralization during which organic products are completely removed. *Enamel* is a synapomorphy of osteichthyans; it probably originated on the scales of early osteichthyans (like *Andreolepis*) and subsequently expanded across the other components of the dermal skeleton.
Dentine	Dentine is the primary tissue of the vertebrate dermal skeleton; like enamel it is both odontogenic and skeletogenic. *Dentine* is a tubular mineralized tissue produced by odontoblasts that generally remain outside the mineralized matrix, which is, however, penetrated by odontoblast cell processes (*i.e.* dentinal tubules radiating from pulp cavities). *Dentine* is produced in two sequential phases; synthesis and deposition of an organic matrix known as predentine followed by its definitive mineralization by hydroxyapatite. In osteichthyans, the *dentine* is of orthodentine type (the cell bodies are located outside the matrix) as opposed to mesodentine (osteostracans and certain 'acanthodians') and semidentine ('placoderms'), which retain odontocytes within the matrix.
Spongiosa	The *spongiosa* is a highly vascularized, parallel-fibered, pseudo-lamellar bone layer, pierced by numerous primary and secondary osteons, and appearing thus as cancellous in certain osteichthyan taxa. When *cosmine* is present, the *spongiosa* is located immediately under the *dentine* layer, the vascular canals (*cross canals*) of the *spongiosa* merging with the horizontal canals (*mesh canals*) of the *dentine*. However, in the absence of *cosmine*, the exposed zones of the *spongiosa* are denser and less vascularized than the deeper regions. Bony tubercles and ridges ornamenting the scales in certain sarcopterygians are also considered to belong to the *spongiosa* as a sculptured external surface.
Isopedine	The *isopedine* is a layer of lamellar bone with a plywood-like arrangement of the collagen plies found in the basal portion of the scales of early osteichthyans. The collagen plies can show two types of orientation: orthogonal (as in the 'osteolepiform' *Osteolepis*) or twisted (as in the extant coelacanth *Latimeria*) (Meunier, 1984). Vascular canals can be found in the *isopedine*, although few in number; certain can open to the exterior through pores. The *isopedine* forms the internal surface of the scale. Its thickness and mineralization state can be variable.
Cosmine	*Cosmine* is not a tissue, but a combination of tissues that develops only in the exposed area of the dermal bones, scales and fin rays of osteichthyans (*i.e.* in the interface between dermis and epidermis). In its broader sense, cosmine consists of the association between a layer of *enamel* overlying a layer of *dentine* (*i.e.* an odontode) that contains a characteristic and complex pore-canal network (developed between and around the odontodes). The pore-canal complex can be associated either with multiple odontodes (as primitively present in stem osteichthyans like *Psarolepis* and actinopterygians like *Meemannia*) or with a single layer of odontodes (as in rhipidistian sarcopterygians). The vertical canals of the *dentine* form flask-shaped cavities that open to the surface through pores in the *enamel*. The whole system is closely connected to an underlying layer of dermal bone (*spongiosa*) through vascular canals (*cross canals*) contacting the horizontal canals (*mesh canals*) of the *dentine*.
Eucosmine	*Eucosmine* is introduced here to describe the *cosmine* arrangement present in rhipidistian sarcopterygians. It corresponds to the "true" *cosmine* (*e.g.* Sire *et al.*, 2009) and allows the description of the structure with a single, more conveying word. *Eucosmine* is characterized by a single layer of *enamel* overlying a uniform layer of *dentine* with a well-developed pore-canal system pervading both the *dentine* and the *spongiosa* underneath. Each odontode shows a one-to-one relationship with a pore-cavity, as opposed to the multiodontode type of *cosmine* present in other sarcopterygians (*e.g.* *Styloichthys*). Previous generations of odontodes are no longer associated with the pore-canal complex and are found buried in the *spongiosa*. The uniform layer of *eucosmine* and the presence of buried odontodes hints towards the occurrence of complicated processes of resorption and deposition of *eucosmine* that are still incompletely understood.
Ganoine	*Ganoine* is a shiny, acellular, non-collagenous, hypermineralized tissue of epidermal origin ornamented with microtubercles. The organic matrix of *ganoine* is deposited by ameloblasts and is structurally comparable to *enamel*, thus making both tissues homologous; the sole distinctive trait being the multi-layered arrangement of *ganoine*. *Ganoine* occurs in the ganoid scales of actinopterygians, either associated with an underlying layer of *dentine* (palaeoniscoid scale of early actinopterygians and extant polypterids) or contacting directly the basal bony layer (lepisosteid scale of gars).

Table I. – Continued.

Pore cavity	The *pore cavities* of the cosmine pervade the *dentine* and open to the surface through pores in the *enamel* layer. *Pore cavities* are usually flask-shaped, with a narrow neck close to the pore and a broad base, although certain degree of shape plasticity is known (Fig. 2). The base is incorporated to the *mesh canals* of the *dentine*.
Mesh canal	The *mesh canals* (or dentinal canals) form a series of horizontal connections between *pore cavities* in the *dentine*. The *mesh canal* network runs parallel to the limit between the *dentine* and the *spongiosa* and forms the pore-canal system of the *cosmine*. In certain 'osteolepiforms', the *mesh canals* may communicate with an underlying extension, that can have a bulged shape (basal extension) or form a system of lower mesh canals, parallel to the overlying *mesh canals* (Fig. 2).
Cross canal	The *cross canals* (or vascular canals) pervade the upper portion of the *spongiosa*. The cross canal network connects with the *mesh canals* (or with the basal extensions) through small vertical canals located under the *pore cavities* and with the pulp cavities of the *dentine* from which dentinal tubules spread. The extension of the *cross canal* complex through the *spongiosa* is variable, depending on its thickness.

2009) (Tab. I). Cosmine is thus not simply considered as a single tissue, but as a combination of tissues (enamel, dentine, and bone) and a structure (pore-canal system).

No living vertebrate bears cosmine and, therefore, the study of its biology (formation, resorption process, function, etc.) is one of the most intriguing and exciting questions in early vertebrate palaeontology (*e.g.* Thomson, 1975; Janvier, 1996). Cosmine is found as a covering of the dermal bones and scales of Paleozoic sarcopterygians and it has been generally considered a strongly supported synapomorphy of Sarcopterygii (*e.g.* Rosen *et al.,* 1981; Meinke, 1984; Cloutier and Ahlberg, 1996; Friedman and Brazeau, 2010), but its absence in many sarcopterygian taxa indicates multiple and convergent losses within the clade (Fig. 1). Previous histological studies and illustrations on cosmine are known from: *Megalichthys* (Williamson, 1849; Goodrich, 1907; Gross, 1956; Thomson, 1977; Borgen, 1989), *Porolepis, Dipterus, Latvius*, *Osteolepis* and 'osteolepidids' indet. (Gross, 1956, 1966), dipnoans indet. (Ørvig, 1969a), *Dipnorhynchus* (Thomson and Campbell, 1971), *Ectosteorhachis* (Thomson, 1975), *Chirodipterus* and *Rhinodipterus* (Gross, 1956; Bemis and Northcutt, 1992), *Uranolophus* (Campbell and Barwick, 1988), *Youngolepis, Powichthys* and *Diabolepis* (Chang and Smith, 1992), *Cladarosymblema* (Fox *et al.,* 1995), *Gogonasus* (Long *et al.,* 1997), *Styloichthys* (Zhu *et al.,* 2006, 2010), *Meemannia* (Zhu *et al.,* 2010; Lu *et al.,* 2016a), *Heimenia* (Mondéjar-Fernández and Clément, 2012) and *Psarolepis* (Qu *et al.,* 2013a, 2016). The different manifestations of cosmine in sarcopterygians were reviewed by Meinke (1984) and hypotheses on cosmine formation and possible function were developed by Ørvig (1969a), Thomson (1975, 1977), Borgen (1989, 1992), and Bemis and Northcutt (1992), among others.

In dermal bones, cosmine often occurs in large sheets that extend over numerous otherwise separate ossifications (*e.g.* individual bones of the skull roof and lower jaws), covering the sutures between them. In the scales, cosmine occupies the exposed field. Goodrich (1907) defined the cosmoid scale as organised in three layers, from dorsal to ventral: a thin layer of enamel (or enameloid), a layer of dentine (comprising a pore-canal system), and a layer of dermal bone composed of a variable-sized layer of vascular bone (spongiosa) and a basal layer of lamellar bone (isopedine) (Tab. I). Usually restricted to rhomboid cosmoid scales (Goodrich, 1907; Francillon-Vieillot *et al.,* 1990; Schultze, 2015), cosmine can also be found in other scale morphotypes (*e.g.* among dipnomorphs in the rounded scales of lungfishes like *Dipterus* and the porolepiform *Heimenia*) (Ørvig, 1969b; Ahlberg and Trewin, 1995; Mondéjar-Fernández and Clément, 2012). However, when present, cosmine is generally found across the entire squamation of the animal, including the trunk and fin bases, despite variations in scale morphotype and size.

The segmented bony fin rays (lepidotrichia) of cosmine-bearing sarcopterygians also possess a cosmine covering. However, the occurrence of cosmine (and other odontogenic manifestations including enamel and dentine derivatives) is restricted to the exposed surface of both scales and lepidotrichia, thus in the portion of the scales and rays directly contacting the epidermis. The overlapped area of the scales and the deeply buried proximal and unjointed portion of the lepidotrichia, which is always covered by the scales in osteichthyans, do not show cosmine (*e.g.* Jarvik, 1980). The resemblance of the small lepidotrichial segments with the trunk scales suggests that scales and lepidotrichia share a deep homology of their developmental features (*e.g.* Baudelot, 1873; Goodrich, 1904; Jarvik, 1959; Schaeffer, 1977; Zylberberg *et al.,* 2010, 2015).

Although cosmine is functionally a full constituent of the dermal skeleton, it is topographically and, to a great extent, developmentally independent of the underlying components (Thomson, 1975). However, since cosmine is viewed as a combination of tissues and a structure, the formation of cosmine does not occur 'altogether', but rather represents an orchestrated development of enamel, dentine, and vascular bone that become intimately bound together. The dermal

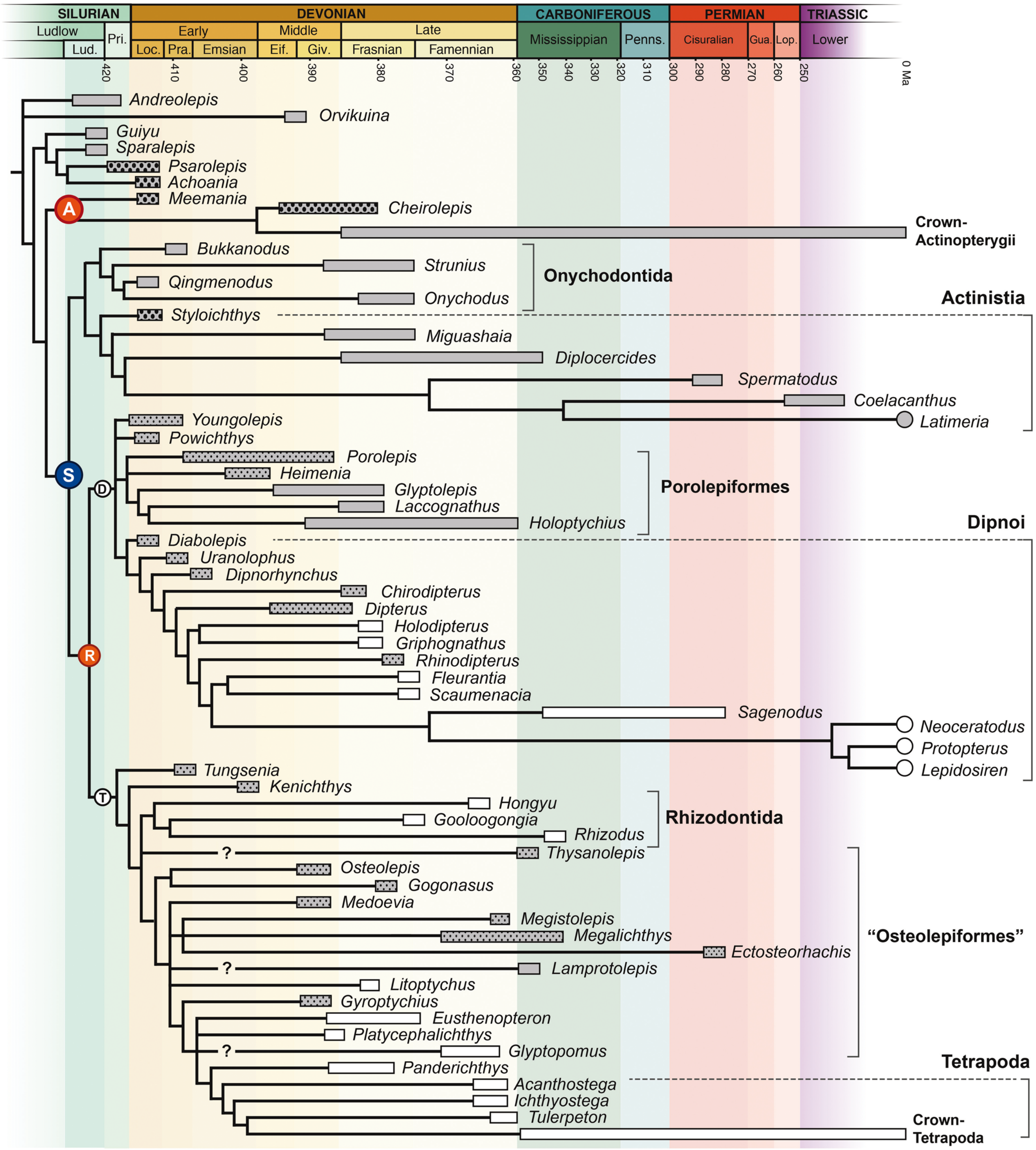

Figure 1. – Interrelationships and geological time range of selected osteichthyans (histologically surveyed taxa or with important phylogenetic implications). Phylogenetic hypothesis after Ahlberg and Johanson, 1998; Johanson and Ahlberg, 2001; Zhu *et al*., 2001, 2006, 2009, 2017; Friedman, 2007; Snitting, 2008; Lu and Zhu, 2010; Coates and Friedman, 2010; Lu *et al*., 2012, 2017; Choo *et al*., 2017, among others. The dates of origin of clades are hypothetical. Abbreviations: A: Actinopterygii, D: Dipnomorpha, R: Rhipidistia, S: Sarcopterygii, T: Tetrapodomorpha. Legends: light grey with large dots: primitive type of cosmine as described in early osteichthyans (presence of large pores associated with a variably developed pore-canal system in the dentine and superimposed odontodes); light grey with fine dots: eucosmine (presence of minute pores associated with a pore-canal system in the dentine overlaid by a single layer of enamel); light grey: odontogenic derivatives of cosmine: ganoine (in actinopterygians), tubercles solely made of dentine or a combination of enamel and dentine (early osteichthyans and sarcopterygians); white: bony ornamentation (absence of odontogenic tissues in the dermoskeleton).

bone and odontogenic tissues (enamel and dentine) forming the pore-canal system are essentially independent systems that are thought to have become juxtaposed, although our understanding of the evolutionary stages of this assembly is still fragmentary. Nevertheless, this perspective allows independent variation of the two systems during ontogeny and points toward an evolutionary relationship between early manifestations of cosmine and other forms of odontogenic ornamentation of the dermal skeleton in early osteichthyans (Meinke, 1984).

Here, I review the current knowledge of the origin, structure, development and possible function of cosmine based on published and new data on the scales and dermal bones of osteichthyans. New data and phylogenetic interpretations of early osteichthyan fossils have challenged the "classical" definition of cosmine, arguing that the term is to become obsolete due to the variability of "cosmine-like" manifestations in taxa such as *Meemannia* (Lu *et al.,* 2016a), *Cheirolepis* (Giles *et al.,* 2015a) and *Psarolepis* (Qu *et al.,* 2013a, 2016), among other early osteichthyans. I will illustrate the difficulties in categorizing cosmine based on these data on early sarcopterygians and actinopterygians and the variability of cosmine types and derivatives as seen in sarcopterygians. Finally, I will present new histological data on derived sarcopterygians that will be helpful for future anatomical and phylogenetical studies in addressing new histological character combinations and primitive features previously unknown in certain clades, highlighting the importance of histology for phylogenetic reconstructions.

MATERIAL AND METHODS

The main sources of information come from published data on the dermoskeleton of Paleozoic early osteichthyans and sarcopterygians. New and previously unpublished data come from thin sections of fossil sarcopterygians scales from the Paleontological Institute of the Academy of Sciences (PIN) in Moscow, Russia (kindly provided by François Meunier during the PhD of the author) and from porolepiform material from Latvia housed at the Museum für Naturkunde (MfN) in Berlin, Germany. Paleohistological cross-sections of the Russian material were performed by François Meunier at the Université Pierre et Marie Curie (UPMC) and porolepiform scales were sectioned at the Muséum national d'Histoire naturelle (MNHN) in Paris, France. All cross-sections were examined under natural transmitted and polarized light with a Zeiss Axiovert35 microscope at the UPMC.

Institutional abbreviations: MfN, Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University, Berlin, Germany; MNHN, Muséum national d'Histoire naturelle, Paris, France; PIN, Paleontological Institute of the Academy of Sciences of Russia, Moscow, Russia; UPMC, Université Pierre et Marie Curie, Paris, France.

THE EVOLUTIONARY ORIGIN OF COSMINE

Traditionally, since the studies of Goodrich (1907), the squamation of osteichthyans has been divided into two scale-types matching the actinopterygian/sarcopterygian dichotomy. Actinopterygians were described as possessing ganoid scales, which are covered with ganoine, a composite tissue defined as a multi-layered enamel covering without intervening dentine layers and the absence of pore canals or a pore-canal network (Richter and Smith, 1995). On the other hand, sarcopterygians were described as possessing cosmoid scales covered with cosmine, which, as opposed to ganoine, is formed by an enamel-dentine complex in which an enamel layer is always associated with an underlying layer of dentine (Sire *et al.,* 2009) (Tab. I). This 'archetypical' division of osteichthyans into ganoid and cosmoid scales has encompassed histological and phylogenetic studies throughout the last century (*e.g.* Janvier, 1996; Sire *et al.,* 2009; Schultze, 2015) with cosmine and ganoine being considered as opposite and exclusive terms, with no clear evolutionary link between them, thus making phylogenetic polarization of ganoine and cosmine not possible.

Similarly, despite thorough histological descriptions of cosmine (*e.g.* Williamson, 1859; Goodrich, 1907), its evolutionary origin remained elusive in the 19th and 20th centuries due to the lack of a recognizable pre-cosmine condition found in the fossil record (Rosen *et al.,* 1981). Pore-canal systems similar to that of cosmine have been described in osteostracan 'agnathans' (*Tremataspis*) (Denison, 1951) and 'acanthodians' (*Poracanthodes*) (Gross, 1956). However, in osteostracans and 'acanthodians', the pore-canal network is morphologically distinct to that of cosmine; the canals are solely enclosed in dermal bone and the vertical cavities open to the surface through pores in an enamel-like layer of dentine (*schmelzartige oberste Dentinschicht*, Gross, 1956). Phylogenetic studies indicate that the pore-canal systems in osteostracans, 'acanthodians', and sarcopterygians might represent parallel experiments in evolution and are thus not considered homologous (Meinke, 1984; Friedman and Brazeau, 2010; Qu *et al.,* 2013a, b, 2015, 2016; Schultze, 2015).

The discovery of early osteichthyans in the Silurian and Lower Devonian of China (*e.g.* Zhu *et al.,* 2006) and the advances in microtomographic paleohistology (*e.g.* Qu *et al.,* 2016) have recently furnished new information on the assembly of histological characters in early osteichthyans and have started to alleviate the problem of cosmine origins. These new Chinese osteichthyans are represented by a yet unnamed onychodont-like form (Zhu and Zhao, 2005), the dipnomorphs *Youngolepis* (Chang and Yu, 1981), *Diabolepis* (Chang and Yu, 1984) and *Arquatichthys* (Lu and Zhu, 2008), the putative actinistian *Styloichthys* (Zhu and Yu, 2002), the actinopterygian *Meemannia* (Zhu *et al.,* 2006), the putative sarcopterygian *Megamastax* (Choo *et al.,* 2014), and the stem osteichthyans *Guiyu* (Zhu *et al.,* 2009), *Sparalepis* (Choo *et al.,* 2017), *Psarolepis* (Yu, 1998; Zhu et al., 1999), and *Achoania* (Zhu *et al.,* 2001) thus furnishing a phylogenetically diverse glimpse of character distribution in early osteichthyans and allowing histological characters in osteichthyan phylogenies to be polarized. Of these taxa, histological studies have focused on the lower jaw of *Youngolepis* (Chang and Smith, 1992), the dermal skull of *Diabolepis* (Chang and Smith, 1992), the dermal skull of *Meemannia* (Zhu *et al.,* 2006, 2010; Lu *et al.,* 2016a), the dermal shoulder girdle of *Styloichthys* (Zhu *et al.,* 2006), the lower jaw of *Guiyu* (Zhu *et al.,* 2009), and the dermal skull and scales of *Psarolepis* (Zhu *et al.,* 2006; Qu *et al.,* 2013a, 2016). The dermal bones and scales of these forms are covered with a shiny layer of enamel bearing large pores and cross sections illustrated the occurrence of a pore-canal complex in the dentine, characterizing cosmine (Zhu *et al.,* 2006), except for *Guiyu* (Zhu *et al.,* 2009) and *Sparalepis* (Choo *et al.,* 2017) presenting enamel-covered ridges and lacking a pore-canal system.

However, histological surveys of *Meemannia*, *Psarolepis* and *Styloichthys* have shown that the pore-canal system in these forms is embedded in several superimposed layers of enamel and dentine, where each superimposed odontode carries a single layer of enamel, thus not corresponding strictly to the ganoine of actinopterygians, but similar to it by the superimposed arrangement of layers (Zhu *et al.,* 2006, 2010). This condition is different to the classically known "true" cosmine of more derived sarcopterygians where a single layer of enamel overlays the dentine and highlights that these taxa exhibit a primitive type of cosmine and a mosaic condition of both "ganoid" type (with multiple generations of odontodes and enamel) and "cosmoid" type histology (Zhu *et al.,* 2006, 2010). The dermal skeleton of these Chinese forms likely represents the pre-cosmine condition and sheds new light on the origin of cosmine. These new data have challenged the previous and "classical" distinction between the ganoid scales of actinopterygians and the cosmoid scales of sarcopterygians (Goodrich, 1907).

A similar condition to that of Chinese stem osteichthyans has also been observed in the dermal bones of the actinopterygian *Cheirolepis* from the Late Devonian of North America and Europe. In the *C. trailli* material from Scotland (Lu *et al.,* 2016a), pore openings on the surface of the bone are continuous with pore cavities and are linked with horizontal canals, with a composite dentine and enamel layer overlying a basal layer of lamellar bone, thus resembling cosmine as found in early sarcopterygians. Previous histological studies on *Cheirolepis* had focused on the scales, where multi-layered enamel (*i.e.* ganoine) was clearly developed (Pearson and Westoll, 1979; Pearson, 1982) in the so-called "palaeoniscoid scales" (an early type of ganoid scale), consisting of a superficial layer of ganoine overlying the dentine and a thick basal layer of lamellar bone (Goodrich, 1907; Sire *et al.,* 2009; Schultze, 2015). However, even Goodrich (1907: 757, fig. 15) in its original description of the palaeoniscoid scales spoke of a layer of "cosmine-like" layer of dentine located beneath the multi-layered enamel and above the lamellar bone layer. The dentine of the palaeoniscoid scale is also pervaded by numerous horizontal canals (Aldinger, 1937; Schultze, 2015), which open to the surface through pores between ganoine ridges (as probably present in *Sparalepis*, Choo *et al.,* 2017) or through the ganoine layer (as illustrated by Goodrich (1907) in the actinopterygian *Eurynotus*). Moreover, a "cosmine-like" organisation of odontogenic tissues has also been reported in the actinopterygian *Paphosiscus* from the Early Carboniferous of Montana, USA (Grogan and Lund, 2015) in which a pore-canal system is embedded in the dentine and elasmodine (a presumably dentine-derived tissue) (Sire *et al.,* 2009) and large pores open to the surface through a single layer of enamel (as opposed to ganoine from other actinopterygians). These occurrences of a pore-canal system in actinopterygians (albeit variable in its composition among taxa) and superimposed layers of enamel and dentine in early osteichthyans suggest that a pore canal network is a shared feature of actinopterygians and sarcopterygians and that multi-layered enamel (ganoine) might derive from these superimposed organization of odontodes as present in stem osteichthyans.

A pore-canal system has also been found outside crown osteichthyans in the stem osteichthyan *Andreolepis* (Qu *et al.,* 2013b, 2016). However, the homology between the canal system of *Andreolepis* and early actinopterygians and the canal system of the cosmine in sarcopterygians still remains unclear. When present, the pores (or canals) occurring in the outer surface of the scales of early osteichthyans (such as *Andreolepis*) and actinopterygians (*e.g. Cheirolepis*, *Moythomasia* and *Raynerius*) (Giles *et al.,* 2015b) are ascending from the horizontal canals located at the limit between the dentine and the lamellar bone (Goodrich, 1907) and they have been considered to belong to the bony tissue (cross canals) rather than to the dentine (mesh canals) as in cosmine (Qu *et al.,* 2016) (Tab. I). Nevertheless, further histological surveys of early actinopterygians are needed to confirm this. A mesh canal system, connecting the pore cavities and pervading the dentine is considered to be absent in early actinopterygians where canals are thought to belong to the bony tissues and thus these pores cannot be homologues with the pore cavities of the pore-canal system of the sarcopterygian cosmine. Moreover, ascending canals pierce several generations of enamel and dentine layers in early actinopterygians like *Meemannia* and *Cheirolepis* (Lu *et al.,* 2016a) and stem osteichthyans like *Psarolepis* (Qu *et al.,* 2013a, 2016), while each pore cavity is incorporated into a single enamel layer in the cosmine of rhipidistian sarcopterygians (Zhu *et al.,* 2010) (Fig. 2).

The homology between the system of horizontal canals in the scales of osteichthyans (either of odontogenic or bony origin) is still unresolved and, therefore, the distinction between the cosmoid and the ganoid scales as present in both early sarcopterygians and actinopterygians is not clear-cut. New interpretations suggest a more patchy distribution of features in the initial stages of evolution of both groups of osteichthyans. A "cosmine-like" organisation of the odontogenic products and associated dermal bone, as well as a pore-canal network in the dermoskeleton, should thus be considered a synapomorphy of osteichthyans, and not strictly restricted to sarcopterygians, with a precursor of both cosmine and ganoine present in the last common ancestor of actinopterygians and sarcopterygians (Lu *et al.,* 2016a; 2017).

Actinopterygians and sarcopterygians thus share a deep common pattern of odontode superposition with an associated pore-canal system. Enamel-associated dentine disappeared in actinopterygians with the establishment of multilayered enamel (*i.e.* ganoine) and pore-canal systems (as primitively present in *Meemannia*) followed in early actinopterygians crownward of *Cheirolepis* (Lu *et al.,* 2016a). By contrast, in sarcopterygians, dentine was retained but associated with a single layer of enamel, the ensemble becoming tightly linked to a complex set of canals pervading the dentine and connecting with the underlying dermal bone. However, as opposed to actinopterygians, the dentine layer in the scales of sarcopterygians contacts a thick and densely vascularized layer of dermal bone (spongiosa), whereas in the scales of early actinopterygians the "cosmine-like" layer of dentine and enamel rest directly upon a layer of lamellar bone (isopedine) where the vascular layer appears to be missing. However, small fractions of vascular bone have been described underneath the dentine in the dermal bones of *Meemannia* (Zhu *et al.,* 2010: figs 5, 6). The spongiosa of *Meemannia* is reduced and not uniformly distributed as seen in the cross sections, thus hinting at its complete disappearance in more derived actinopterygians such as *Cheirolepis* for which no vascular bone layer have been described so far.

Now that a "cosmine-like" organisation of the odontogenic tissues of the dermoskeleton no longer defines the Sarcopterygii, a thick vascular bone region (spongiosa) with well-developed cross canal network may be used as a diagnostic synapomorphy of sarcopterygians, although its presence, albeit reduced, in the dermal bones of *Meemannia* (Zhu *et al.,* 2006, 2010) suggest that a vascular bony layer might have also been present in the common ancestor of crown osteichthyans. The "stepwise" evolution of cosmine from early forms such as *Psarolepis* and *Styloichthys*, and its relationships with the underlying spongiosa, can now be followed until the establishment of eucosmine in rhipidistians (dipnomorphs and tetrapodomorphs).

THE DEVELOPMENT OF COSMINE

Our understanding of the formation and subsequent remodelling of cosmine during ontogeny is unclear. The scales of osteichthyans are considered polyodontode, capable of growth by the addition of new generations of odontodes, as opposed to non-growing monodontode scales as present in chondrichthyans (Janvier, 1996). An odontode can be described as a tooth-like module composed of dentine surrounding a pulp structure (canal or cavity) being generally capped by an enamel or enameloid layer (Reif, 1982).

Cosmine, and other odontogenic tissues are known to be capable of resorption during growth of the animal (Francillon-Vieillot *et al.,* 1990). Westoll (1936) first realized the necessity of resorption of cosmine to accommodate the growth of the dermal skeleton. Subsequent studies on cosmine occurrence and growth (*e.g.* Jarvik, 1948, 1950; Gross, 1956; Ørvig, 1969a; Thomson, 1975, 1977) suggested that each cosmine sheet represents a single depositional event. Cosmine was thus considered to be laid down by an essentially undivided cosmine field in the dermis and not as fused odontodes (*contra* the "lepidomorial theory" of Stensiö and Ørvig, see Janvier, 1996 and Donoghue, 2002), but early sarcopterygians like *Psarolepis* show traces of what could represent earlier ontogenetic and phylogenetic stages when the pore-canal system was becoming organized under the form of isolated or superimposed dentine tubercles capped with enamel (Qu *et al.,* 2016).

The occurrence in adult cosmine of "ontogenetic traces" is informative on the development and arrangement of cosmine during growth. Smith (1977) suggested that a dermal ornamentation composed of separated odontodes of dentine and enamel might represent the primitive condition in sarcopterygians. A single cosmine sheet was then acquired in certain taxa and further evolutionary changes might have proceeded in two directions: (1) preserving only the cosmine sheet, as in 'osteolepidids' and 'porolepidids', or (2) retaining the early ontogenetic stage of separated odontodes (denticles) and no cosmine, characteristic of holoptychiids, derived dipnoans, onychodontids, and actinistians (crownward of *Styloichthys*). The organization of the cosmine in *Meemannia* (Zhu *et al.,* 2006), *Styloichthys* (Zhu *et al.,* 2010) and *Psarolepis* (Qu *et al.,* 2013a, 2016) has refuted the primitive condition of isolated tubercles as proposed by Smith (1977), and certainly implied by Ørvig (1968, 1969a), but showed that the occurrence of a pore-canal system is

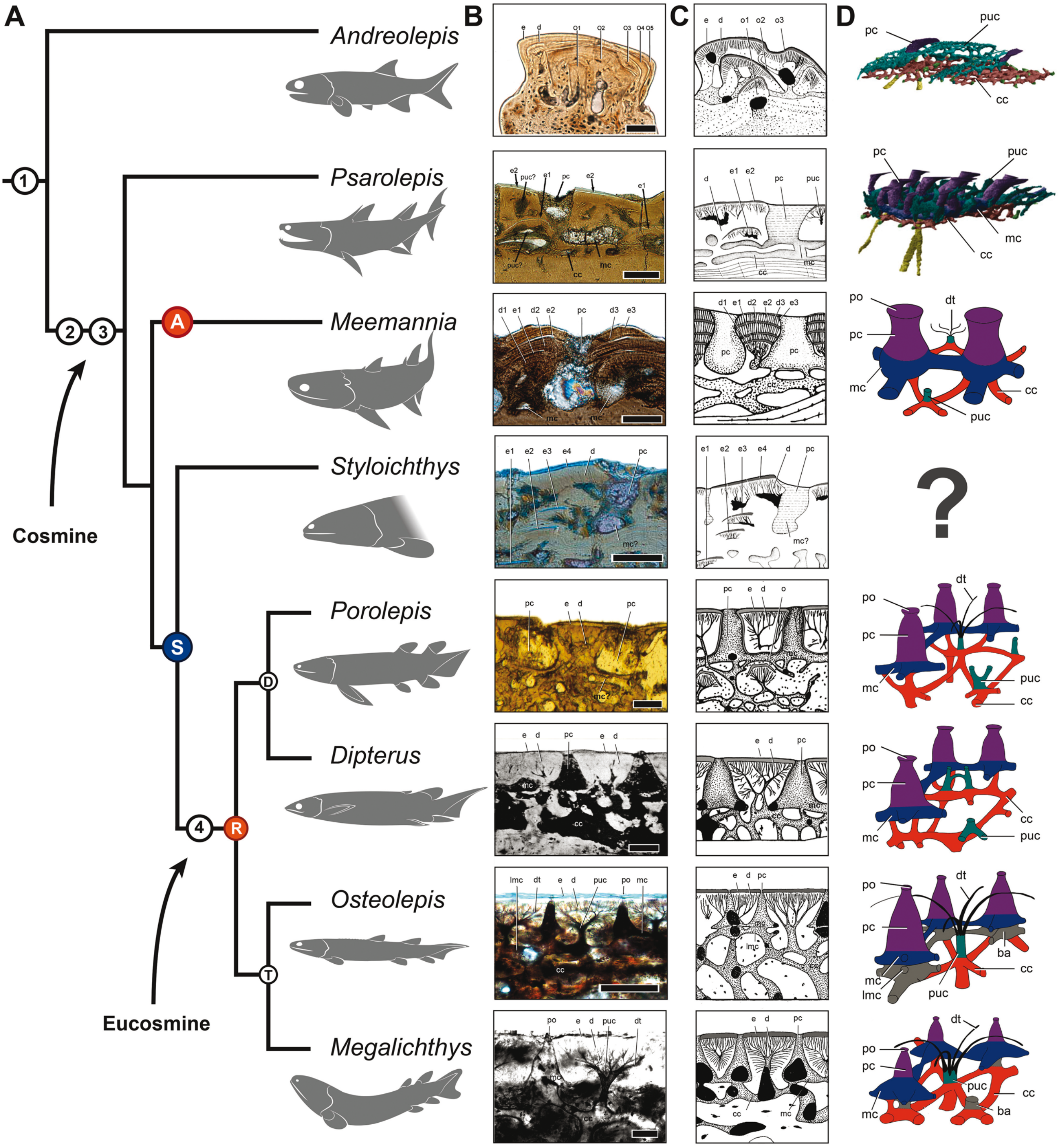

Figure 2. – Phylogenetic implications and evolutionary scenario of cosmine development in osteichthyans. Numbers 1-4 detailed in the text (Development of cosmine). **A**: phylogenetic interrelationships of selected osteichthyans (after Lu et al., 2017) and interpretative reconstructions of taxa; **B**: histological cross sections; **C**: illustrations of the histological structures from the cross sections; **D**: virtual and idealized reconstructions of the pore-canal system of the cosmine. Sources of cross sections and drawings: *Andreolepis*: Zhu *et al*., 2010, Qu *et al*., 2013b, 2016; *Psarolepis*: Qu *et al*., 2013a, 2016; *Meemannia:* Zhu *et al*., 2010; *Styloichthys:* Zhu *et al*., 2006; *Porolepis:* Gross, 1956; Mondéjar-Fernández and Clément, 2012; *Dipterus*: Gross, 1956; *Osteolepis*: Gross, 1956, Schultze, 2015; *Megalichthys:* Gross, 1956; Thomson, 1975. Scale bar = 100 μm. Abbreviations: ba, basal extension; cc, cross canal; d, dentine; dt, dentinal tubules; e, enamel; lmc, lower mesh canal; mc, mesh canal; od, odontode; pc, pore cavity; po, pore opening; puc, pulp cavity.

tightly linked to the structure and arrangement of the odontodes.

The work of Qu *et al*. (2013a, b, 2016) on *Andreolepis* and *Psarolepis* through the first time use of microtomography in the study of the formation and arrangement of odontogenic tissues in the dermoskeleton of early osteichthyans enabled to propose a new developmental scenario for the assembly of cosmine in sarcopterygians. Although the authors cautioned that the conclusions have to be considered provisional, a general scenario based on their work can be described. This preliminary scenario can be tested with further histological surveys of fossil material (Fig. 2).

(1) *Stem osteichthyans* (like *Andreolepis*): the scales of very early osteichthyans are ornamented with ridge-like odontodes. The first-formed odontodes lie above the horizontal canals of the bony base of the scale, and new odontodes are added sequentially, either on top or beside older odontodes (Qu *et al.,* 2013a, b, 2016). This pattern of odontode deposition is maintained in early actinopterygians; the evolution of multi-layered enamel (*i.e.* ganoine) is a consequence of this odontode superposition and subsequent loss of the dentine component of the odontode.

(2) *Stem osteichthyans* (like *Psarolepis*): the odontodes formed after the primordial ridge-like odontode are different in shape and larger than the narrow primordial odontode and lead to the loss of a ridge-like ornamentation of the scales replaced by a uniform cosmine covering with a smooth layer of enamel. This change of shape and general organisation of the odontogenic tissues of the dermoskeleton might be due to a significant change in the epithelium-mesenchyme system. Unfortunately given the absence of similarly arranged odontogenic products in extant forms it is currently impossible to understand the causes of such changes. This transition from ridge-like odontodes to "larger" odontodes is considered the first key step in the assembly and evolution of cosmine in sarcopterygians. A similar condition might also be present in *Meemannia* but further histological 3D study is needed to confirm it.

(3) *Stem and crown osteichthyans*: in the scales of *Psarolepis*, sarcopterygians (like *Styloichthys*) and actinopterygians (like *Meemannia*) the larger odontodes are associated with a pore-canal system, suggesting that the establishment of the association between odontogenic tissues (dentine and enamel) and a complex pore-canal system is an osteichthyan synapomorphy. However, in these taxa, new odontodes are produced and added atop of older odontodes, without a single one-to-one relationship with a pore-cavity or the entire pore-canal network, indicating that the odontogenic portion of the scales can grow in thickness without affecting the organisation of the pore-canal system. Older generations of odontodes (either associated with a pore-canal system as in *Meemannia* or not as in *Orvikuina*) do not show significant traces of resorption or reworking in the basal layers, near the contact with the underlying bony base. However, in sarcopterygians, older generations of odontodes are found buried in the lower-most part of the dentine layer and can show some partial resorption (as seen in *Styloichthys* and *Psarolepis*) but still remain associated with the pore-canal system of the cosmine.

(4) *Sarcopterygian rhipidistians* (dipnomorphs and tetrapodomophs): a uniform cosmine covering is found in many taxa (*e.g*. 'porolepidids' like *Porolepis,* and *Heimenia*, 'osteolepiforms' like *Osteolepis, Gyroptychius, Gogonasus, Megalichthys*, etc.) (*e.g.* Gross, 1956; Jarvik, 1985; Mondéjar-Fernández and Clément, 2012). This cosmine arrangement displays a single layer of enamel overlaying a uniform layer of dentine with a well-developed pore-canal system pervading both the dentine and the vascular bone underneath. In the primitive type of cosmine (*e.g. Psarolepis*, *Meemannia* and *Styloichthys*), earlier generations of odontodes had the ability to induce the formation of new, younger generations of odontodes that became superimposed. In more derived sarcopterygians, the epithelium-mesenchyme system might have undergone a new change with the ability to secrete a continuous sheet of cosmine, probably simultaneously along large surfaces of the dermoskeleton. This cosmine condition encountered in Rhipidistians is here termed eucosmine (*i.e.* "true" cosmine) (Tab I). Odontode superposition does not occur in the dentine layer of eucosmine and buried odontodes are absent from the cosmine layer. Older generations of odontodes can be found in the spongiosa with clear signs or resorption and reworking, however further histological survey of rhipidistian fossils is needed to understand the phylogenetic distribution of this feature.

Given our current understanding of the sarcopterygian phylogeny (and considering *Styloichthys* a basal coelacanth), we might assume that the presence of buried odontodes in the dentine layer is primitive for sarcopterygians and present in early sarcopterygians below the rhipidistian node (Fig. 2). Rhipidistians might retain older generations of odontodes below the cosmine layer, buried in the spongiosa (*e.g.* the dipnomorphs *Powichthys, Porolepis*, *Dipterus*, *Uranolophus*) (Gross, 1956; Bystrow, 1959; Meinke, 1984; Chang and Smith, 1992). Moreover, in these taxa, the anterior portion of the exposed area of the scales is covered in denticles, usually with a horse-shoe shape, made of dentine and enamel. These denticles (*i.e.* odontodes) spread along the anterior edge of the cosmine, marking the limit between the overlapped and exposed areas of the scales. As Bystrow (1959: figs 10, 11) showed in the scales of *Porolepis uralensis*, the denticles can either be located at the same level of the cosmine or at a lower level in the vascular bone layer. In other dipnomorphs like *Uranolophus* and *Porolepis*, the isolated denticles buried beneath the cosmine sheet are exposed to the surface in areas devoid of cosmine cover, indicating that ridge-like primordial odontodes, like the odontodes of the *Psarolepis* scale, were also present in these taxa. As suggested by the formerly described developmental scenario, isolated odontodes predate the acquisition of a single cosmine sheet, both ontogenetically and phylogenetically. Evidences for this can be found in the cosmine-covered dipnomorphs *Uranolophus* and *Porolepis* but also in *Glyptolepis* and *Laccognathus*, which lack cosmine in the scales but retain numerous buried odontodes in the spongiosa (Bystrow, 1939) (Fig. 3).

This puzzling condition suggests that early rhipidistians might have retained the ability to produce small odontodes as well as large cosmine sheet. This condition is more usually found in the scales of dipnomorphs than in tetrapodomorphs; in the former, the cosmine sheet breaks into minute denticles anteriorly, whereas in the latter the cosmine field shows more straight margins and no signs of buried odontodes in the spongiosa. However, the developmental orchestration of this combined occurrence of eucosmine and isolated odontodes needs more histological survey in key rhipidistian taxa, such as the early tetrapodomorphs *Tungsenia* and *Kenichthys* (Zhu and Ahlberg, 2004; Lu *et al.*, 2012) in order to understand how a polyodontode state of the cosmine (the primitive type of cosmine as present in early osteichthyans) evolved into a continuous shield of cosmine (eucosmine) in rhipidistians. The role of resorption is key to explain these different manifestations.

Thomson (1975) description of cosmine ontogeny in the megalichthyid ‘osteolepiform’ *Ectosteorhachis* from

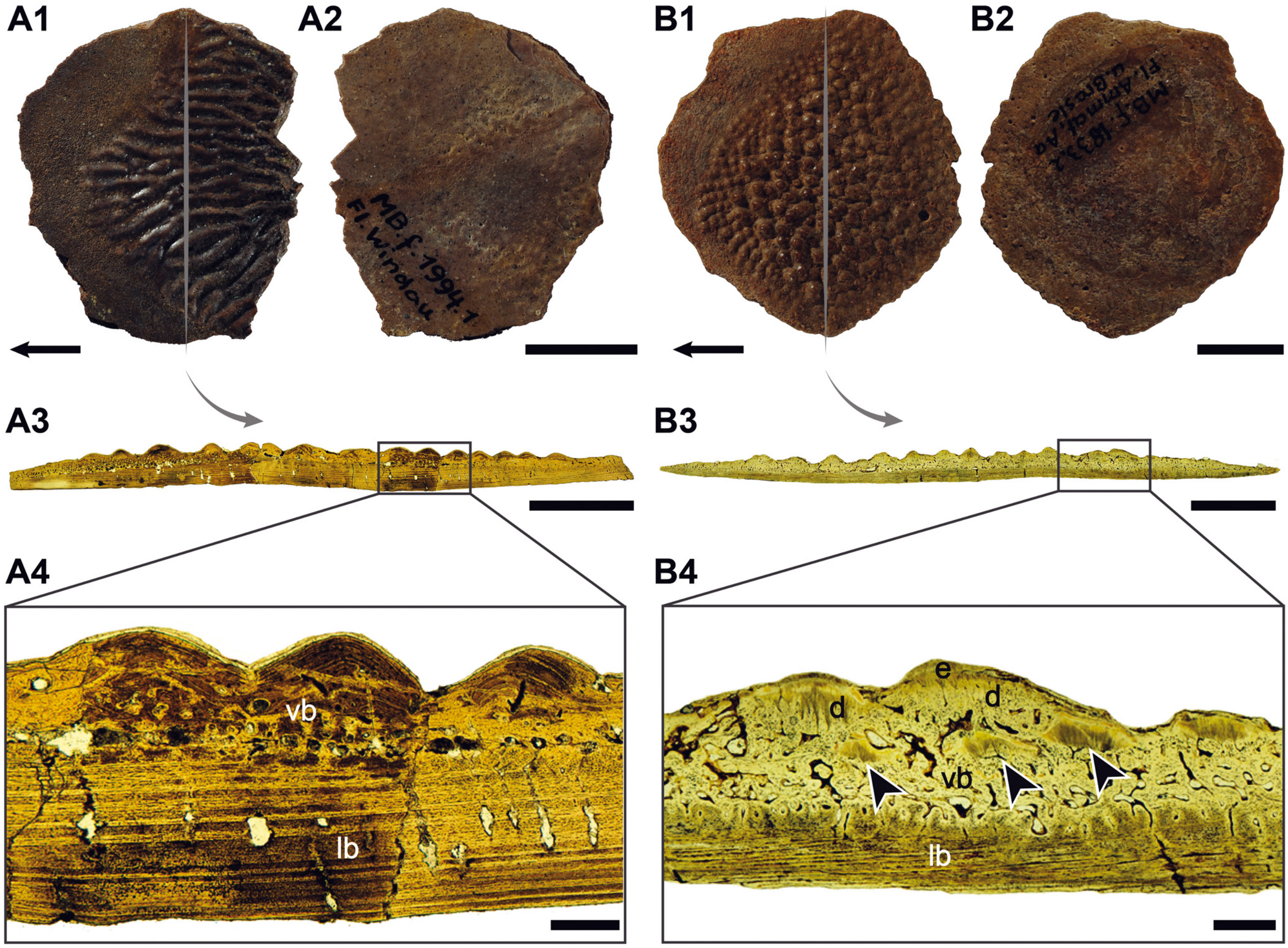

Figure 3. – Morphology and histology of porolepiform holoptychiid scales. **A**: *Holoptychius nobilissimus* (MB.f. 1994.1) and **B**: *Laccognathus panderi* (MB.f. 1833,2) from the Middle – Late Devonian of Latvia. 1: External view of the scales (arrow points anteriorly); 2: Internal view of the scales; 3: General view of the cross section; 4: Inset from the cross section showing the arrangement of the histological layers. Note the ornamental and histological differences between both scales: in *Holoptychius* the exposed area is ornamented with thick longitudinal ridges solely made of dense bone resting upon the spongiosa (vascular bone); in *Laccognathus* the exposed area shows numerous dentine tubercles, capped with a thin enamel layer (*i.e.* odontodes), older odontodes from previous generations are embedded in the underlying spongiosa (black arrowheads). In both scales, the internal surface is flat and smooth and is solely formed by the isopedine (lamellar bone) layer, which is relatively thicker in *Holoptychius* than in *Laccognathus*. Abbreviations: d, dentine; e, enamel; lb, lamellar bone; vb, vascular bone. Scale bars: A/B2 = 1 cm; A/B3 = 5 mm; A/B4 = 500 µm.

the Early Permian of Texas, USA illustrated that cosmine resorption is a dynamic process tuned with growth. He proposed that cosmine was laid down around patches of the developing pore-canal mosaic in larval or juvenile fishes. By the addition of patches, and after perhaps several episodes of resorption and redeposition as the pore-canal system formed its interconnections, the fish became completely covered with cosmine. In *Ectosteorhachis* then, the pore-canal network and hard tissues apparently developed simultaneously, and, later in ontogeny, this pattern was altered in various ways. However, these observations might solely concern *Ectosteorhachis* (or 'osteolepiforms' more generally); a uniform scenario of eucosmine formation, integrating the deposition and putative resorption of older layers of cosmine is needed but currently lacking for rhipidistians.

The loss of cosmine observed in several sarcopterygian groups is considered to have produced vertical canals, communicating the vascular canals of the spongiosa with the exterior. Such canals have been noticed in *Glyptolepis* (Ørvig, 1957) and similar ones were described in the gastral scales of the Permian tetrapod *Australerpeton* (Dias and Richter, 2002). However, in tetrapods these are probably not homologous with the vertical pore cavities of the cosmine pore-canal system, since odontogenic components are absent in the scales of tetrapods (Witzmann, 2011; Mondéjar-Fernández *et al.,* 2014) (Fig. 1), but with openings of the vascular canals of the spongiosa and were probably related to oxygen intake through the scales (Witzmann *et al.,* 2010). In groups in which early representatives were covered with cosmine, but lost it in derived members (*e.g.* porolepiforms) these canals might be considered as remnants of the pore cavities of the cosmine (Tab I). The canals present in *Glyptolepis* were tentatively interpreted as mucous canals by Ørvig (1957: fig. 5), thus consistent with one of the possible functions of the cosmine cavities.

THE FUNCTION OF COSMINE

The most challenging aspect of studying cosmine concerns its function in living fishes. Since no extant sarcopterygian representative possesses cosmine, clues on its possible function might be found in the structure of the pore-canal complex, resorption processes, and ontogenetic development in fossil forms. Proposals on the function of cosmine have been numerous, but the great majority of early studies assigned to the cosmine a role in the housing of sensory organs (*e.g.* Moy-Thomas, 1971; Thomson, 1975, 1977; Northcutt and Gans, 1983; Meinke, 1984). For these authors, pore-canal systems, as present in 'agnathans', 'acanthodians', and sarcopterygians, primarily had a sensory (possibly electro-sensory) function; the pore-canal cavities would have housed a series of electroreceptory ampullary organs. However, certain studies on sarcopterygians have challenged this view.

Fox *et al.* (1995) proposed that the cosmine pore-cavities in the 'osteolepiform' *Cladorosymblema* might have been sites of mucus-secreting cells, reprising Ørvig hypothesis on the porolepiform *Glyptolepis* (1957). Bemis and Northcutt (1992) showed that the skin from the snout of the extant lungfish *Neoceratodus* contains horizontal plexuses and vertical capillary loops with similar structure, size and density to the components of the cosmine from the dermal bones of the skull in Paleozoic dipnoans such as *Dipterus* and *Chirodipterus*. Similarly, Borgen (1992) proposed that the pore-canal system of the cosmine, at least in 'osteolepidids' and porolepiforms, could have primarily functioned as a vascular system and that the pore-canal cavities might have contained a vascular loop or a sinusoid. Zhu *et al.* (2010) showed that in *Meemannia*, the multiple layers of superimposed odontodes coexisting with one pore-canal network indicates that the pore-canal network does not have a one-to-one relationship to any single odontode layer. Moreover, sensory pores are larger and often occur in clusters in certain specific regions of the body (usually the snout and ventral region), whereas cosmine pores are minute, extremely numerous and distributed throughout the entire squamation and dermal bones of the animal (Bemis and Northcutt, 1992).

These observations cast serious doubt on the belief that cosmine bears sensory and/or glandular function, which was inferred from the unique association of the pore-canal network with one single layer of odontodes and enamel in rhipidistians. Moreover, Meinke (1984) pointed out that electroreceptory ampullary organs do not communicate directly with each other. Thus, the system of horizontal canals of the dentine (mesh canals) connecting the vertical pore cavities is an argument against an electroreceptive function of the pore-canal cavities. Therefore, the primitive condition described in *Meemannia, Styloichthys* and *Psarolepis* is more consistent with the function of cosmine as a vascular complex involved in the deposition and resorption of mineralized tissues, as proposed by Borgen (1992) and Bemis and Northcutt (1992). Eucosmine as present in rhipidistians (where older, partially resorbed odontodes might be present in the spongiosa) should thus be considered under the 'resorption and deposition' functional view; the early explanation of cosmine as a 'sensory' tissue should be avoided. A sensory function might have been performed by other pore-canal systems with larger pores, located mainly in the snout (*e.g.* see Campbell *et al.,* 2010) or related to the lateral line.

The hypothesis that the main function of the pore-canal system is to facilitate the deposition and resorption of odontogenic tissues fits into the proposal that the dermal skeleton functions as a store for calcium and phosphates (Donoghue *et al.,* 2006). The role of cosmine in the metabolic regulation of mineral ions was thoroughly studied by Thomson (1975) in *Ectosteorachis*. Based on the occurrence of a diverse set of cosmine manifestations (*e.g.* blisters, tubercles, complete cosmine covering, etc.), Thomson proposed that such manifestations might have been due to seasonal resorption of the cosmine in connection with a need to make large volumes of calcium and phosphates available, for instance for reproduction, as well as in connection with growth of the dermal skeleton. *Ectosteorhachis* may have had an anadromous behaviour, and migrated between sea and fresh water to breed. Cosmine resorption would have taken place in fresh water environments, depleted from food resources and minerals compared to the sea. A similar scenario was also proposed for the Cretaceous actinopterygian *Lepidotyle* (Meunier and Gayet, 1992) showing traces of ganoine resorption. Recently, Schultze (2015) challenged the occurrence of resorption in *Ectosteorhachis* and *Megalichthys* after re-studying the material. However, a 3D survey of the dermoskeleton might be the only way to ascertain and properly identify resorption processes (Qu *et al.,* 2016; S. Sanchez, pers. comm.).

Nevertheless, this scenario might be too simplistic when we consider the occurrence of cosmine and cosmine derivatives in other sarcopterygians. Devonian, cosmine-bearing sarcopterygians (*e.g.* basal actinistians, 'porolepidids', early dipnoans, and 'osteolepidids') seem to be restricted to mostly fully marine environments (*e.g.* Yunnan and Gogo sites) (Xun *et al.,* 1996; Long and Trinajstic, 2010). In these forms, cosmine is always well developed and no traces of important resorption due to migrations, as proposed by Thomson (1975), are seen. These would confirm Thomson's view that cosmine covering was always continuous in sea environments. However, the 'osteolepiforms' *Osteolepis* and *Gyroptychius* from the Devonian of Scotland (Jarvik, 1985) and *Cladarosymblema* from the Carboniferous of Australia (Fox *et al.,* 1995) possess a rather continuous cosmine covering and have been referred to a freshwater environment (lacustrine and fluviatile) as well as the Early Devonian porolepiform faunas (Ørvig, 1969a; Mondéjar-Fernández and Clément, 2012) from Spitsbergen (Friend and Moody-Stuart, 1973), although putative areas of resorption have been observed. Moreover, possible counterexamples are Devonian marine onychodontids (*e.g. Qingmenodus* and *Onychodus*) (Andrews *et al.,* 2006; Lu *et al.,* 2016b) and actinistians (*e.g. Euporosteus*) (Zhu *et al.,* 2012), which appear to have lost cosmine very early in their evolutionary history (Friedman, 2007; Lu and Zhu, 2010). Nevertheless, onychodontids and actinistians, as well as certain holoptychiids, show dentine tubercles, some of which are capped with enamel; the odontogenic component of the dermoskeleton was thus retained in these marine forms (Ørvig, 1957; Castanet *et al.,* 1975).

Curiously, sarcopterygian taxa devoid of cosmine or any other type of odontogenic tissue (*e.g.* certain holoptychiids, derived dipnoans, rhizodontids, tristichopterids, 'elpistostegalians', and tetrapods) have not been found in totally marine environments, but rather in marine-influenced, lagoonal, deltaic, or even freshwater environments (*e.g.* Lebedev and Coates, 1995; Johanson and Ahlberg, 2001; Cressler *et al.,* 2010). It seems that in these forms, a non-fully marine habitat is related to the loss of odontogenic components of the dermoskeleton, thus hinting towards a causal explanation for the absence of odontogenic tissues in non-marine environments. Further studies on these taxa should focus on the paleoenvironment and ion content of the water in order to determine whether this hypothesis is consistent (*e.g.* Cloutier *et al.,* 2011).

The remaining question is: what could be the advantage of the retention of dentine and enamel (either via cosmine or isolated odontodes) in a marine environment? After Thomson (1975) proposition that dentine was a mean of calcium and phosphate storage in anadromous fishes, cosmine would have been produced in salt water where these ions are in excess and resorbed in time of short supply or need under certain life conditions, especially when these fishes left the sea to dwell in fresh waters. Resorption processes are highly demanding in energy. Possibly cosmine disappeared convergently in sarcopterygians when certain groups adapted to a more fresh-water environment and found other ways of storing ions without needing to resorb mineral tissues. Interestingly, when considering the convergent loss of cosmine with regard to the stratigraphical distribution of the taxa, a pattern emerges: cosmine was lost independently in the majority of sarcopterygian clades during the Early to Middle Devonian (Fig. 1). Some notable exceptions, including 'porolepidids' and megalichthyid 'osteolepiforms' retain a cosmine covering until the Late Devonian and even until the late Paleozoic (*e.g. Ectosteorachis*). However, the reasons for this remain unclear. Future studies should consider the environmental constraints and global climatic variations during the Devonian and check whether the loss of odontogenic components of the dermal skeleton is somehow related to changes in the ionic content of marine and/or fresh waters (*e.g.* Long *et al.,* 2016).

Thomson (1975) suggested that the presence of a continuous cosmine covering is an ontogenetic character present in reproductive mature individuals. Westoll (1936) and White (1965) reported the absence of cosmine in small specimens of *Dipterus* and so did Ørvig (1969a) in small dipnoans indet. from the Middle Devonian of Bergisch-Gladbach, Germany. In *Porolepis* or *Uranolophus*, early generations of odontodes can be seen under the continuous cosmine covering, distributed around the pore-canal cavities (Gross, 1956; Campbell and Barwick, 1988). Later in ontogeny, a cosmine sheet was laid down, encasing the pore-canal system and overlying the odontodes that were subject to progressive internal resorption. Cosmine thus develops late in ontogeny. Therefore, the loss of cosmine has been viewed as a paedomorphic trait in sarcopterygian evolution (Bemis, 1984). The study of cosmine development can furnish key information in our understanding of ontogenies in fossil osteichthyans (Cloutier, 2010).

An interesting aspect of the histological consequences of the loss of cosmine concerns the fate of the spongiosa, which henceforth becomes exposed as constituting the most external portion of the superficial portion of the scales. Thomson (1975) stated that in the scales of *Ectosteorhachis* the zones of the exposed area devoid of a cosmine covering (either due to a more important growth of certain parts of the scale or partial resorption of the cosmine) the naked spongiosa is denser and less vascularised that in normal conditions. Such a dense spongiosa strongly resembles the condition present in the bony scales of porolepiforms like *Holoptychius* (Fig. 3), early tetrapods such as *Tulerpeton* (Mondéjar-Fernández *et al.,* 2014) and the outer portion of the superficial region of the scales of *Eusthenopteron* (Zylberberg *et al.,* 2010). However, in *Tulerpeton*, the vertical canals of the spongiosa are not present, whereas in *Eusthenopteron* they can occur (Jarvik, 1980). A denser upper part of the spongiosa could have played a role as a reinforcement against mechanical wear of the upper exposed area, or as a way of creating a smoother surface, as seen in the anterior overlapped area of the scales, which is solely composed of bone (spongiosa and isopedine), regardless of the scale morphotype and the histological structure of the exposed area.

In relation to wear, a common explanation to the distribution of cosmine deals with its role as a sort of "shield" in parts of the body that could have been more exposed to contact with the substrate (Clément, 2004). However, in all fishes, the dermal skeleton is not "naked", or totally exposed to the environment. The bones of the skull, fins, and scales are overlain by the epidermis, which in the vast majority of cases secretes a mucus improving water penetration and minimizing injuries caused by rough substrate contact. Even if cosmine appears to be more developed in the ventral region of the body and anterior portion of the snout in certain taxa (*e.g. Porolepis*, *Heimenia*, dipnoans, etc.), it does not necessarily mean that these regions were more "protected" from injuries by the presence of cosmine. The skin, which is a living tissue with nervous connections, would have been continuously wounded, producing not only pain to the animal, but also implicating a regular healing, which is an energy-consuming process. I propose instead that the presence of "thicker" cosmine in these regions could have had a role in slightly increasing the weight of the ventral region and the anterior tip of the snout in benthic fishes as a resistance against buoyancy and therefore, facilitating a benthic predatory behaviour as usually suggested for many early sarcopterygians (Janvier, 1996; Clack, 2002).

DISTRIBUTION AND PHYLOGENETIC IMPLICATIONS OF COSMINE IN SARCOPTERYGIANS

Cosmine has proved to be an adaptable tissue-complex that can lead to different configurations of odontogenic tissues (*e.g.* spoon-shaped tubercles, blisters, Westoll lines, etc.). Primitively present in early osteichthyans (see above), cosmine distribution and manifestations in sarcopterygians have usually been of taxonomic use in the reconstruction of sarcopterygian interrelationships and the attribution of new fossil remains to certain groups. Here, I will briefly review the occurrence of cosmine and other odontogenic derivatives in histologically-surveyed sarcopterygians to illustrate the diversity of dentinous and bony tissues present in the dermoskeleton of lobe-finned fishes; these diverse manifestations and their evolutionary implications in our understanding of sarcopterygian interrelationships will also be discussed.

Cosmine in sarcopterygians

Early osteichthyans – The basal portion of the sarcopterygian tree was occupied by a consistent clade of early sarcopterygians known as psarolepids or the "*Guiyu* clade", comprising the Chinese forms *Guiyu*, *Achoania*, *Psarolepis* and *Sparalepis* (Choo *et al.,* 2017). However, they have been recently reconstructed as stem osteichthyans, based on the discovery of the early sarcopterygian *Ptyctolepis* (Lu *et al.,* 2017). In the rhombic scales of *Psarolepis*, a primitive form of cosmine is present, represented by superimposed odontodes and a pore-canal system, illustrating the early evolutionary stages of the build-up of cosmine, as described in early actinopterygians like *Meemannia* (previously considered a sarcopterygian) (Zhu *et al.,* 2006, 2010) and *Cheirolepis* (Lu *et al.,* 2016a). In *Psarolepis*, odontodes from previous generations are found buried in the dentine layer (Qu *et al.,* 2013a, b, 2016). However, the pores in the enamel of the rhombic scales in *Psarolepis* (and other early osteichthyans, like *Andreolepis*) are larger than the fine pores as seen in crownward sarcopterygians. Cosmine has also been reported in *Achoania* (Zhu *et al.,* 2001) and in the putative sarcopterygian *Megamastax* (Choo *et al.,* 2014), although no histological study or phylogenetic reconstructions were furnished for this last taxon.

Onychodontids – Onychodontids are not well known, and few histological details of their dermoskeleton are available. The scales of all known onychodontids are rounded in shape and they are ornamented along the entire exposed area of the scale with ridges or spoon-shaped tubercles probably made of dentine (*e.g. Onychodus*) (Andrews *et al.,* 2006); the presence of enamel (or enameloid) is unclear (Janvier, 1996). Small patches of cosmine have been reported in the parietal and premaxilla of *Strunius* from the Middle Devonian of

Germany (Jessen, 1966, 1967) but no histological data have been published to confirm it. The most basal onychodontid, *Bukkanodus* from the Early Devonian of Australia (Johanson *et al.,* 2007) shows a dermal ornamentation comprising fine pores and vermiform ridges, as well as small denticles on the scales. Unpublished thin sections confirmed the absence of enamel and a pore-canal system, thus ruling out the presence of cosmine in *Bukkanodus*. However, the earliest onychodontid *Qingmenodus* from the Early Devonian of China (Lu and Zhu, 2010; Lu *et al.,* 2016b) shows a dermal ornament of tiny pores, much smaller and more closely spaced than in *Bukkanodus*, but no histological data are available; the scale shape is also still unknown in this taxon. The presence of cosmine in onychodontids thus remains uncertain at the moment. New data from the onychodont-like Chinese form (Zhu and Zhao, 2005), covered with a shiny coat of enamel and pores are eagerly awaited.

Actinistians – The actinistians (or coelacanths *sensu lato*) possess a reduced dermoskeleton and a rather uniform pattern of dermal ornamentation. The scales of actinistians are rounded in shape. They are ornamented with coarse or thin ridges distributed on the exposed area of the scales that break into spoon-shaped tubercles (as in onychodontids) in the anterior margin of the exposed area (*e.g. Latimeria,* Roux, 1942; Smith *et al.,* 1972; Castanet *et al.,* 1975; Smith, 1979; Meunier, 1980). This ornamentation pattern of both the scales and dermal bones is uniformly maintained in all actinistians from the Paleozoic to Recent (*e.g. Gavinia, Miguashaia, Diplocercides, Nesides, Undina, Rhabdoderma, Whiteia, Piveteauia, Macropoma, Coelacanthus, Swenzia* and *Latimeria*) (Stensiö, 1937; Schaeffer, 1941; Forey and Young, 1985; Cloutier, 1996a; Forey, 1998; Forey *et al.,* 2000; Clément, 1999, 2005; Long, 1999), however the histological nature of the ridges and tubercles is unclear since no comparative histological work has been done on coelacanth scales (Forey, 1998). The ridges have been reported to be made of dentine in Paleozoic forms like *Diplocercides* from the Late Devonian (Gross, 1933) and Mesozoic forms like *Undina* from the Jurassic (Gross, 1933) and *Macropoma* from the Cretaceous (Williamson, 1849), whereas the ridges of *Chagrinia* from the Late Devonian (Schaeffer, 1962) were described as made of bone. The scales and dermal bones of *Diplurus* from the Triassic (Schaeffer, 1952) were tentavily reported as being covered with a thin layer of enamel, but absent from the ridges and tubercles. The denticles found in the dermal bones of *Spermatodus* from the Permian are composed of dentine and enamel (*i.e.* odontodes) (Westoll and Romer, 1939; Meinke, 1982) with several layers of denticles overlapping each other and evidence of resorption and redeposition of bone and denticles as part of the growth process. Dentine-made ridges capped with enamel are also present in the extant *Latimeria* (Castanet *et al.,* 1975). The putative basal actinistian *Styloichthys* (Zhu & Yu, 2002; Friedman, 2007) is exceptional among coelacanths: it presents a primitive type of cosmine and rhombic scales, two conditions different from those of other known, more derived forms. The currently considered most primitive actinistians *Gavinia* from the Middle Devonian of Australia (Long, 1999) and *Miguashaia* from the Late Devonian of Canada (Cloutier, 1996a) do not possess cosmine and both show rounded scales with the classical ornamentation formerly described.

Dipnomorphs

Besides the well-defined clades of the Porolepiformes and the Dipnoi, several uncertainly located taxa are gathered among the Dipnomorpha. *Powichthys* from the Early Devonian of Canada and Spitsbergen (Jessen, 1975; Clément and Janvier, 2004) has been interpreted either as the sister taxon of dipnomorphs (Forey, 1998), dipnoans (Ahlberg, 1991; Cloutier and Ahlberg, 1996; Zhu *et al.,* 2001), or porolepiforms (Clément and Janvier, 2004; Clément and Ahlberg, 2010). *Youngolepis* from the Early Devonian of China (Chang and Yu, 1981; Chang, 1982) was described as a stem dipnoan and, along with *Diabolepis* they would represent two successive sister groups of the Dipnoi. *Arquatichthys* from the Early Devonian of China (Lu and Zhu, 2008) and *Langdenia* from the Early Devonian of Vietnam (Janvier and Phuong, 1999) have been considered as stem dipnomorphs, although with caution. All these taxa have rhombic scales covered with cosmine, although only *Youngolepis* and *Powichthys* have been histologically surveyed and possess eucosmine (Chang and Smith, 1992).

Porolepiforms – The dermal ornamentation of porolepiforms is morphologically and histologically diverse. The squamation of ‘porolepidids’ is composed of thick rhombic scales covered with eucosmine (*Porolepis, Heimenia, Durialepis*) whereas in holoptychiids the scales are thin, rounded, and lack cosmine (*e.g. Holoptychius*) (Ørvig, 1969b; Jarvik, 1980; Janvier, 1996; Otto, 2007). The condition of *Heimenia* is informative on the evolutionary transformation of the squamation between ‘porolepidids’ and holoptychiids (Mondéjar-Fernández and Clément, 2012). The extent of the enamel layer is variable in dipnomorphs: in certain dipnoans and in *Youngolepis*, *Powichthys* and *Diabolepis* (Chang and Smith, 1992) the enamel layer extends half way into the cosmine pores, in *Porolepis*, the enamel lines the entire surface of the pore-cavity, and in *Heimenia* the enamel does not penetrate the pores but rather forms a slightly bulged margin (Mondéjar-Fernández and Clément, 2012). The complete loss of odontogenic components appears to be phylogenetically gradual in holoptychiids; basal members such as *Glyptolepis* and *Laccognathus*, retain a series of superimposed odontodes made of dentine and enamel (Gross, 1956; Bystrow, 1959; Jarvik, 1972), whereas *Holoptychius* (consider to be more derived) (Schultze, 2000) possesses scales completely made of bone, excepting some possible small dentine tubercles anteriorly (Fig. 3) and buried odontodes in the dermal bones of the skull (Bystrow, 1939). Moreover, it is possible that *Glyptolepis* could show remnants of the pore-canal system, as proposed by Ørvig (1957), but further histological survey of this taxon in needed in order to confirm or refute it.

Dipnoans – The dermoskeleton of dipnoans is also variable in its ornamentation. The earliest forms show rhombic (*e.g. Uranolophus*) or rounded scales (*e.g. Dipterus*) with patches or a continuous cosmine covering. Dipnoan eucosmine is characterized by the presence of more or less concentric lines of discontinuity in the enamel, the so-called Westoll lines, which are interpreted as being due to cyclic resorption and redeposition during growth (Ørvig, 1969a) and are a distinctive feature of the group (present in *Diabolepis*) (Chang and Smith, 1992). *Uranolophus* from the Early Devonian of North America (Denison, 1968a, b) and *Dipnorhynchus* from the Early-Middle Devonian of Australia (Thomson and Campbell, 1971) display cosmine on the skull roof bones and in the rhombic scales. The cosmine in these taxa grades into a series of ridges and tubercules anteriorly and shows Westoll lines. The denticles on the scales are solely made of dentine and are located around the edge of the exposed surface, a condition similar to that of cosmine-covered porolepiforms, usually in a lower plane than the uniform cosmine layer. Buried odontodes are also present in the spongiosa (Meinke, 1984). Cosmine can co-occur in the rounded scales and dermal bones, or solely in the skull and snout of other Devonian taxa such as *Dipterus* (Forster-Cooper, 1937; Ahlberg and Trewin, 1995), *Rhinodipterus* and *Ganorhynchus* (Gross, 1956), *Nielsenia* (Lehman, 1959), *Sunwapta* (Thomson, 1967), *Chirodipterus* (Miles, 1977), *Stomiahykus* (Bernacsek, 1977), *Speonesydrion* (Campbell and Barwick, 1983), *Gogodipterus* (Long, 1992), *Iowadipterus* (Schultze, 1992), *Sorbitorhynchus* (Wang *et al.,* 1993), *Ichnomylax* (Long *et al.,* 1994), *Erikia* (Chang and Wang, 1995), *Pillararhynchus* (Barwick and Campbell, 1996*), Tarachomylax* (Barwick *et al.,* 1997), *Jessenia* (Otto and Bardenheuer, 1997), *Adololopas* (Campbell and Barwick, 1998), *Melanognathus* (Schultze, 2001), *Orlovichthys* (Krupina *et al.,* 2001), *Dipnotuberculus* (Campbell *et al.,* 2002), *Amadeodipterus* (Young and Schultze, 2005), *Cathlorhynchus* (Campbell *et al.,* 2009), *Harajicadipterus* (Clement, 2009), *Sinodipterus* (Qiao and Zhu, 2009), *Robinsondipterus* (Long, 2010), and *Pinnalongus* (Newman and den Blaauwen, 2014) . In several of these taxa, isolated denticles co-occur with continuous cosmine sheets and Westoll lines. *Griphognathus* (Schultze, 1969a) and *Holodipterus* (Miles, 1977) do not show a cosmine covering in the dermal bones but external denticles are present in some bones combined with buried odontodes; small putative cosmine patches and odontodes are also known in the scales of the ventral region of *Griphognathus*, the rest being ornamented by bony ridges (Smith, 1977). From the Late Devonian onwards, lungfishes show a tendency towards bone reduction (in the endo- as well as in the dermoskeleton) and loss of the cosmine (*e.g. Fleurantia*, *Scaumenacia*, *Holodipterus*, *Sagenodus,* etc.) (Miles, 1977; Cloutier, 1996b; Schultze and Chorn, 1997). The extant forms (*Neoceratodus, Lepidosiren* and *Protopterus*) show rounded scales ornamented with fine, slightly undulating bony ridges and no odontogenic tissues (Kerr, 1955; Brien, 1962).

Tetrapodomorphs

Tungsenia from the Early Devonian of China (Lu *et al.,* 2012) is the earliest representative of the Tetrapodormorpha and the sister group of all other tetrapodomorphs, although solely known by dermal skull and lower jaws bones covered by a thick layer of cosmine. Another Chinese form, *Kenichthys* from the Middle Devonian is known by well-preserved skull and pectoral girdle material and scales (Chang and Zhu, 1993; Zhu and Ahlberg, 2004). *Kenichthys* possesses cosmine on its dermal bones and rhombic scales, which are similar to that of rhombic-scaled ‘osteolepiforms’, with a marked antero-dorsal groove between the overlapped and exposed surfaces. Unfortunately, these two early tetrapodomorphs have not been histologically surveyed.

Rhizodontids – Dermoskeletal ornamentation is surprisingly uniform in rhizodontids; ornamentation of the dermal bones and scales is mainly composed of fine bony ridges and tubercles. The scales of all known forms are rounded in shape, with a pointed posterior end in certain taxa (*e.g. Gooloogongia*) (Johanson and Ahlberg, 2001). Rhizodontids represent the most basal Devonian radiation of tetrapodomorphs, however, they show remarkably specialized features convergent with other groups of Devonian tetrapodomorphs very early on as seen in *Hongyu* from the Late Devonian of China (Zhu *et al.,* 2017). Cosmine (or any other type of odontogenic tissues) is unknown in rhizodontids, despite its presence in early tetrapodomorphs like *Kenichthys* and *Tungsenia* (Chang and Zhu, 1993; Lu *et al.,* 2012). No histological studies of their dermal skeleton have yet been performed, excepting the study of the dentine in their teeth (*e.g. Rhizodus* and *Strepsodus*) (Schultze, 1969b). However, new redescriptions of uncertainly placed ‘osteolepiforms’ that can turn out to be rhizodontids (*Thysanolepis* in Coates and Friedman, 2010) might show evidence of cosmine in primitive members of the Rhizodontida (see below).

‘*Osteolepiforms*’ – The ornamentation of the dermoskeleton of ‘osteolepiforms’ is among the most variable in sarcopterygians. Certain ‘osteolepidids’ (*e.g.* megalichthyids, *Osteolepis*, *Gyroptychius*, etc.) possess cosmine-covered rhombic scales, whereas other derived forms (*e.g. Canowindra*, tristichopterids) show rounded scales lacking cosmine (Ahlberg and Johanson, 1998; Snitting, 2008). The rhombic scales of 'osteolepidids' differ from other rhombic scales (*e.g.* porolepiforms) by the presence of a well-marked groove that separates the overlapped and exposed areas, the absence of tubercles anterior to the cosmine sheet of the exposed area (as in *Kenichthys*) (Chang and Zhu, 1993), and a different density and size of the cosmine pores. Cosmine covered 'osteolepiforms' include *Osteolepis*, *Gyroptychius* and *Thursius* (Gross, 1956; Jarvik, 1985), *Thaumatolepis* (Obruchev, 1941), *Megistolepis* (Obruchev, 1955), *Megalichthys* (Gross, 1956), *Sterropterygion* (Thomson, 1972), *Latvius* (Jessen, 1973), *Ectosteorhachis* (Thomson, 1975), *Criptolepis* (Worobjewa, 1975), *Megapomus* and *Thysanolepis* (Vorobyeva, 1977), *Chrysolepis* (Lebedev, 1983); *Gogonasus* (Long, 1985), *Beelarongia* (Long, 1987), *Koharalepis*, *Platyethmoidea*, *Vorobjevaia* and *Mahalalepis* (Young *et al.,* 1992), *Medoevia* (Lebedev, 1995a), *Cladarosymblema* (Fox *et al.,* 1995), *Muranjilepis* (Young and Schultze, 2005), *Sengoerichthys* (Janvier *et al.,* 2007), *Owensia* (Holland, 2009), *Palatinichthys* (Witzmann and Schoch, 2012), and *Askerichthys* (Borgen and Nakrem, 2016). As previously reviewed by Meinke (1984) the odontogenic tissues in 'osteolepiforms' can be found in 5 different forms: 1) Complete cosmine-sheets (*e.g. Gogonasus*); 2) Discontinuous cosmine separated by Westoll lines-like areas of naked bone (*e.g.* certain specimens of *Osteolepis* and *Gyroptychius*); 3) Cosmine blisters (*e.g. Ectosteorhachis*); 4) "Mixed" cosmine (unfinished cosmine attributed to early ontogenetic stages) (*e.g. Ectosteorhachis*); 5) Tubercles (*e.g. Ectosteorhachis* and *Lamprotolepis*). These different manifestations can be explained as an either spatial or temporal breakdown of a continuous cosmine sheet as primitively present in early tetrapodomorphs (*e.g. Tungsenia* and *Kenichthys*) (Thomson, 1975). Patches of cosmine have been described in *Rhizodopis* (Andrews and Westoll, 1970) and Thomson (1968) reported dentine ridges in *Hyneria*, although histological data is lacking. All other 'osteolepiforms' lack odontogenic derivatives; the rounded scales and dermal bones of tristichopterids and other derived forms are ornamented with fine bony ridges (as in rhizodontids) or a series of small bony tubercles (*e.g. Eusthenopteron, Canowindra, Litoptychus*) (Denison, 1951; Thomson, 1973; Jarvik, 1980).

'*Elpistostegalians*' + *Tetrapods* – The Elpistostegalia (sensu Daeschler *et al.,* 2006) includes the Middle-Late Devonian paraphyletic assemblage of the 'elpistostegalians' *Tiktaalik* (Daeeschler *et al.,* 2006), *Panderichthys* (Vorobyeva and Lyarskaya, 1968) and *Elpistostege* (Westoll, 1938; Schultze, 1996) and the tetrapods. The clade is characterized by the complete loss of the odontogenic tissues in the dermoskeleton. The scales of 'elpistostegalians' are rhombic in shape but do not possess cosmine; they are ornamented by a series of bony coarse tubercles (Witzmann, 2011). Early tetrapods present a large array of scale morphotypes. Devonian tetrapods (such as *Ichthyostega*, *Acanthostega*, and *Tulerpeton*) (Coates, 1996; Jarvik, 1952, 1996; Lebedev and Coates, 1995) possess rounded, ovoid, or spindle-shaped scales, whereas certain Carboniferous and younger tetrapods show a recovery of a "squared" morphotype different from the plesiomorphic rhombic morphotype of their fish relatives (Witzmann, 2011). Ornamentation is usually absent, the scales being solely composed of bone. Histologically, the scales of tetrapods are extremely simple compared with those of other sarcopterygians; enamel and dentine are absent as well as the basal isopedine layer made of lamellar bone (Mondéjar-Fernández *et al.,* 2014).

New histological perspectives on tetrapodomorph interrelationships

As recently proposed for actinistians based on the histological and phylogenetic survey of *Styloichthys* (Friedman, 2007), the occurrence of cosmine in early members and subsequent loss or replacement in more derived forms of any given sarcopterygian group might be confirmed by new histological data and phylogenetic reconstructions. The case of 'osteolepiforms' is of particular interest amongst sarcopterygians due to their rich fossil record and their currently unresolved interrelationships. Two decades of research following early formative studies of tetrapodomorph relationships (*e.g.* Ahlberg and Johanson, 1998) have yielded conflicting hypotheses (*e.g.* Coates and Friedman, 2010) rather than increased consensus; the current state of "osteolepiform" interrelationships and their bearing among tetrapodomorphs can be accordingly described as chaotic. This phylogenetic uncertainty severely hampers to reconstruct major aspects of tetrapodomorph macroevolution concerning both the endo- and dermoskeleton, ranging from specific sequences of character acquisition, to patterns of convergence, to rates and modes of evolutionary change. Most recent analyses have been restricted to a limited set of early tetrapodomorph fishes, with two major groups from the 'middle part' of the tree ('osteolepidids' and megalichthyids), being largely neglected. A great diversity of early forms, particularly Euramerican taxa, have been shoehorned into these loosely defined assemblages, but remain poorly described despite excellent material. The case of Russian tetrapodomorphs material is greatly relevant for these issues.

Russian tetrapodomorph fishes are represented by obscure material that has been rarely illustrated and mainly published in Russian since the middle of the 20th century (*e.g.* Obruchev, 1941, 1955; Vorobyeva, 1962, 1977; Lebedev, 1983). These taxa (*e.g. Chrysolepis, Criptolepis, Lamprotolepis, Megapomus, Megistolepis, Thaumatolepis, Thysanolepis*, etc.) display morphological and histological disparity. However, detailed accounts are needed under the light of new techniques and phylogenetic interpretations. Histological cross sections at my disposal, furnished by François Meunier, comprised three of these Russian

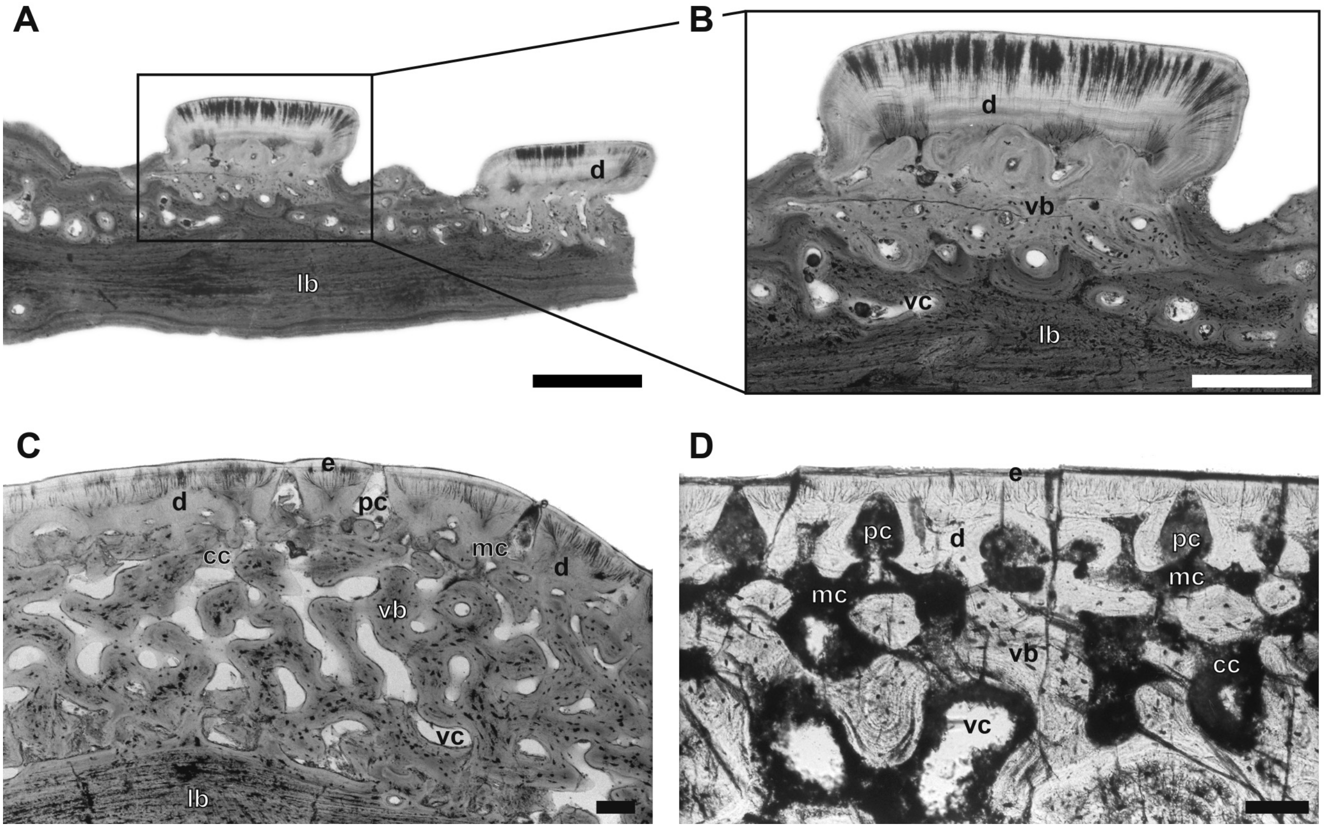

Figure 4. – Histological cross sections of Russian tetrapodomorph scale material. **A**: *Lamprotolepis* (‘Osteolepiformes’), fragment of a scale ornamented with dentine tubercles. **B**: Inset of a tubercle (odontode). Note the absence of a pore-canal system and of enamel capping the dentine tubercle. The odontodes lie on a thin and irregularly developed layer of vascular bone (spongiosa). The basal lamellar bone layer (isopedine) is thick and well developed. **C**: *Thysanolepis* (?Rhizodontida), upper portion of a scale in cross section. Note the presence of cosmine formed by the association of enamel and dentine pervaded by a pore-canal system. The middle vascular bone layer (spongiosa) is well developed and rests on the basal layer of lamellar bone (isopedine). **D**: *Megistolepis* (‘Osteolepiformes’), upper portion of a scale in cross section. Note the presence cosmine and a well developed and cancellous spongiosa. The inferior part of the pore-canal system of the cosmine prolongs itself into the vascular canals of the spongiosa. Basal bony layer not visible. Abbreviations: d, dentine; e, enamel; lb, lamellar bone; mc, mesh canal; pc, pore cavity; vb, vascular bone; vc, vascular canal. Pictures courtesy of François Meunier. Scale bars: A = 1 mm; B = 500 µm; C, D = 100 µm.

tetrapodomorphs with rhombic scales: *Thysanolepis* and *Lamprotolepis* from the Lower Carboniferous (Vorobyeva, 1977) and *Megistolepis* from the Late Devonian (Obruchev, 1955). The description and illustration of their histology is furnished here for the first time (Fig. 4); unfortunately, reference numbers for this material have been lost.

Lamprotolepis – The illustrated scale fragment of *Lamprotolepis* (Fig. 4A, B) shows two well-developed dentine (d) tubercles overlying an irregularly thick layer of vascular bone (vb or spongiosa), which rest on a basal layer or lamellar bone (lb or isopedine). There is no enamel capping of the tubercles. The dentine presents numerous dentinal tubules radiating from the pulp cavities. No pore-canal system is visible, either within the dentine layer or the vascular bone; cosmine can thus be considered absent (*contra* Borgen and Nakrem, 2016). Vascular canals (vc) are present in the spongiosa, stretching ventrally to the margin of the dorsal edge of the isopedine, with the former layer displaying a brighter grey tone than the latter. The basal layer of lamellar bone (lb) is composed of parallel-fibered bone, as clearly visible in the ventral portion, however, the dorsal portion does not show a clear straight margin with the spongiosa: vascular canals occur dorsally in a darker bony tissue than the brighter upper portion of the spongiosa and thus hint towards a putative older deposition of the dark bony tissue at the base of the scale compared with a younger bright bone tissue and dentine tubercles of the upper portion. A vascular canal in the isopedine is also seen ventrally, close to a probable bundle of Sharpey’s fibers (Fig. 4A, inferior to the left). Numerous osteocyte lacunae are visible both in the spongiosa and isopedine layers. The vascular canals show traces of osseous reworking (secondary osteons) (Fig. 4B). Other traces of resorption are difficult to identify, but the irregular dorsal exposed margin of the spongiosa between the two odontodes might have been subject to some resorption process compared with the straighter surface left of the main odontode.

Dentine tubercles margins are rounded, similar to the “finished margins” of unresorbed odontodes in *Ectosteorhachis* (Thomson, 1975). No buried odontodes are visible.

Thysanolepis – The scale possesses eucosmine (Fig. 4C) and displays the typical organisation of the cosmoid scale (Goodrich, 1907), composed of four different layers, from top to bottom: (1) enamel, (2) dentine, (3) middle vascular bone (vb), and (4) basal lamellar bone (lb). The enamel layer (e) is thin and constitutes a single layer. The absence of cellular processes from the underlying dentine layer confirms the presence of enamel, and not enameloid. The enamel layer does not penetrate the pore-cavities of the cosmine (pc). The dentine (d) also shows numerous dentinal tubules radiating from the pulp cavities, roughly orthogonal to the overlying enamel layer. The dentine layer is pervaded by vertical cavities (pc) and horizontal canals (mc, mesh canals) diagnostic of the cosmine. The vertical pore-cavities are conically flask-shaped, resembling the profile seen in other ‘osteolepiforms’ like *Megalichthys* (Fig. 2). The layer of vascular bone (vb) is densely vascularized, the system of canals (cc, cross canals) communicate vertically with the dentine canals. Basal extensions, as seen in other ‘osteolepiforms’ (Gross, 1956; Qu *et al.,* 2016) are weakly developed, although it is not clear whether the cross canals of the spongiosa connect directly with the mesh canals and the pore cavities of the dentine or through the basal extensions, as in *Megalichthys*. The basal layer (lb) is only partially visible but it is clearly composed of parallel-fibered bone. As opposed to *Lamprotolepis*, the dorsal margin separating the spongiosa from the isopedine layer is straight. As in *Lamprotolepis*, numerous osteocyte lacunae are present in the vascular and lamellar bone layers. The vascular canals appear to be formed by primary osteons, no evident traces of resorption of reworking are visible. Buried odontodes are absent.

Megistolepis – The scale fragment is of typical cosmoid type with eucosmine, although the basal layer is not seen in the picture (Fig. 4D). A thin single layer of true enamel (e) overlays the dentine (d) and does not penetrate the pore cavities (pc). Although less marked than in *Lamprotolepis* and *Thysanolepis*, numerous dentinal tubules radiate from large pulp cavities of the dentine (d). As in the eucosmine of *Thysanolepis*, diagnostic flask-shaped vertical cavities (pc) and mesh canals (mc) pervade the dentine. The vascular bone (vb) of the spongiosa is densely vascularized and the cross canals (cc) communicate vertically with the mesh canals (mc) of the dentine, possibly through weakly developed basal extensions as in *Megalichthys*. Osteocyte lacunae occur in the spongiosa. The vascular canals (vc) are primary osteons, traces of resorption of reworking are lacking as well as buried odontodes.

In these cross sections (Fig. 4), *Thysanolepis* and *Megistolepis* present the three different histological layers of the cosmoid scale as present in basal sarcopterygians and similar to the eucosmine of ‘osteolepiforms’ (*e.g. Megalichthys*). However, the condition of *Lamprotolepis* is unique among tetrapodomorphs: the presence of tubercles made of dentine is similar to the holoptychiid condition (*e.g. Laccognathus,* Fig. 3B), whereas in tetrapodomorphs the ridges or tubercles ornamenting the dermoskeleton are known to be solely composed of bone (*e.g.* rhizodontids, tristichopterids, rhizodopsids). In ‘osteolepiforms’, isolated tubercles of odontogenic nature have only been described in *Ectosteorhachis* (Thomson, 1975); however, when present, they were overlain by a thin enamel layer, which is absent in *Lamprotolepis*. Evidences of resorption are scant and further histological exploration is needed on more completely preserved fossil material of *Lamprotolepis* to explain this singular pattern of dermal ornamentation among ‘osteolepiforms’.

Cosmine is present and well developed in the scales of *Thysanolepis* and *Megistolepis*, and the enamel layer does not penetrate the pore cavities, as in other ‘osteolepiforms’. However, their phylogenetic position among tetrapodomorphs is still unresolved. Although *Megistolepis* has been assigned to the family Megalichthyidae (Young *et al.,* 1992; Coates and Friedman, 2010), the position of *Thysanolepis* is more controversial. Young *et al.* (1992) assigned *Thysanolepis* and *Vorobjevaia* from the Late Devonian of Antarctica to the family Thysanolepidae (Vorobyeva, 1977). However, Coates and Friedman (2010) stated that both genera were “probable rhizodonts” (Coates and Friedman, 2010: 402). Examples of previous taxonomical attributions challenged by subsequent studies are known among ‘osteolepiforms’ (*e.g.* the case *Notorhizodon*, previously assigned to the rhizodontids and later described as a tristichopterid) (Young *et al.,* 1992; Johanson and Ahlberg, 2001). A critical new approach to the poorly known Russian ‘osteolepiforms’ is necessary since it might challenge previous taxonomic attributions and alter character distribution among tetrapodomorphs interrelationships.

The case of cosmine is particularly relevant since it is not known in any rhizodontid, including the basalmost representative *Gooloogongia* (Johanson and Ahlberg, 1998). Rhizodontids have rounded scales ornamented by bony ridges, very similar to those of tristichopterids, but certainly acquired by convergence (Ahlberg and Johanson, 1998). However, the recent discovery of the problematic tetrapodomorph *Hongyu* (Zhu *et al.,* 2017) has highlighted the homoplastic nature of many tetrapodomorph features. If future phylogenetic analyses confirm Coates and Friedman supposition about its rhizodontid nature, *Thysanolepis* would constitute the first cosmine-covered rhizodontid, and, given the primitive condition of a cosmine covering in sarcopterygians, would probably be placed as the sister taxon of all other rhizodontids. It is still too soon to make such assertions, but a thorough revision of the Russian sarcopterygian faunas is greatly needed.

A similar case of possible taxonomic and phylogenetical reinterpretation concerns the 'osteolepiform' *Glyptopomus* from the Late Devonian of Scotland (Rosebrae Beds and Dura Den; Jarvik 1950), Pennsylvania (Newberry, 1889), and central Russia (Lebedev, 1995b). The scales of *Glyptopomus* are rhombic in shape but lack cosmine. This condition is known in certain rhizodopsids (*e.g. Rhizodopsis*) (Schultze and Heidtke, 1986) and *Litoptychus* (Denison, 1951; Coates and Friedman, 2010). Moreover, the scales of *Glyptopomus* are ornamented by a series of bony tubercles and small ridges, similar to the condition of the 'elpistostegalians' *Panderichthys*, *Tiktaalik* and *Elpistostege* (Schultze, 1996; Witzmann, 2011, pers. obs.). However, the phylogenetic position of *Glyptopomus* is unknown since no phylogenetic study has yet included it in the data set. Schultze and Chorn (1998) suggested a close relationship with megalichthyids whereas Coates and Friedman (2010) proposed that *Glyptopomus* would lie close to or within the clade comprising tristichopterids, 'elpistostegalians', and tetrapods (Fig. 1). The absence of cosmine alone is insufficient to assign a position to *Glyptopomus* within crownward tetrapodomorphs since it has been lost at least in five tetrapodomorph lineages (*e.g.* rhizodontids, tristichopterids, some canowindrids and rhizodopsids, and 'elpistostegalians' + tetrapods). An almost identical situation was also highlighted by Coates and Friedman (2010) for *Platycephalichthys* from the Late Devonian of Russia and Latvia (Vorobyeva, 1959, 1962), which is certainly a polyphyletic genus (Clément, 2002). Of the two species currently comprised in the genus *Platycephlichthys*, *P. skuenicus* might possess rounded scales (although the material from Skujaine is not articulated and includes both rhombic and rounded scales) and could belong to the tristichopterids, whereas *P. bischoffi* shows rhombic scales without cosmine and thus might be closer to 'elpistostegalians' (Snitting, 2008; Coates and Friedman, 2010). In any case, thorough studies of *Glyptopomus* and *Platycephalichthys* are needed. The inclusion of histological features among other more 'classic' anatomical characters could shed more light on the phylogenetic relationships of these two genera among tetrapodomorphs and bring new data on the histological and morphological transformations close to the emergence of tetrapods.

CONCLUSION

The evolution of the dermoskeleton in general and the squamation in particular in osteichthyans seems to occur on two levels, matching the two main portions of the scales (*i.e.* superficial and basal). These two portions show independent evolutionary trends, thus suggesting separate developmental origins. Indeed, loss of tissues (*e.g.* cosmine) can occur in one portion of the scale without affecting the other. Moreover, the weight of convergence in scale evolution in sarcopterygians has been highlighted; the loss of cosmine in the vast majority of the Devonian groups is among these convergent traits.

Cosmine certainly played an important role as a morphofunctional and physiological component of the dermal skeleton. Unfortunately, given the current knowledge on dermoskeleton development in early vertebrates and the sarcopterygian material at hand, it is not possible to arrive at a definite answer as to how the cosmine system truly formed and functioned. If cosmine formation and structural arrangement of the different tissues composing it are seen as processes subject to heterochronic changes, then the different morphologies resulting from the break up of cosmine present in a variety of sarcopterygian taxa certainly represent changes in the timing of hard tissue and pore-canal development and epithelium-mesenchyme interactions.

The overwhelming amount of data retrieved from the scales of fossil and extant osteichthyans enabled previous studies to name and characterize certain enduring histological terms (*e.g.* cosmine for sarcopterygians, ganoine for actinopterygians, etc.) that have proven to be less restricted than previously thought but rather part of a primitive histological continuum. Moreover, these findings suggest that histological survey must also be carried out on the dermal bones that have been underestimated due to the more abundant and easily accessible scale material, which has proven to be more easily sectioned than "precious" dermal bone material (*e.g. Cheirolepis* in Giles *et al.,* 2015a; Lu *et al.,* 2016a). Microtomographic, non-destructive studies are starting to fill this gap in our knowledge, biased by the more abundant scale data.

Finally, scales and dermal bones should not be deemed as poorly informative structures in the study of early vertebrates, and particularly osteichthyans (Meunier, 2011). The scales of sarcopterygians have proven to possess a valid systematic and phylogenetic value, and their study should be viewed as a useful tool in future evolutionary, paleobiogeographic, and faunal analyses. Taxonomic determination should be based on the presence of different, but associated, scale features (*e.g.* external shape, ornamentation, microstructure) rather than on unique "distinctive" characters (which can be regarded as strongly homoplastic) (*e.g.* lack of cosmine, rounded shape).

Acknowledgements. – I would like to warmly thank Olga Otero (Université de Poitiers) for encouraging me to contribute to this volume celebrating the work of Professor François Meunier. I also thank Gaël Clément and Philippe Janvier (MNHN), Sophie Sanchez and Per Ahlberg (Uppsala University), Zerina Johanson (NHM), Qingming Qu (University of Ottawa) and Sam Giles (University of Oxford) for stimulating discussions on palaeohistology and sarcopterygian diversity, Matt Friedman (University of Michigan) for insights into tetrapodomorph interrelationships and Russian material, Florian Witzmann (MfN) for the loan of fossil scale material, Lilian Cazes (MNHN) for preparing the thin sections, and Louise Zylberberg (UPMC) and Armand de Ricqlès (Collège de France) for access to their microscope. The constructive comments of two anonymous reviewers improved the paper. I would like to dedicate this article to Professor François Meunier for his outstanding contribution to vertebrate histology and his enduring help and interest in my work.

REFERENCES

AHLBERG P.E., 1991. - A re-examination of sarcopterygian interrelationships, with special reference to the Porolepiformes. *Zool. J. Linn. Soc.*, 103: 241-287.

AHLBERG P.E. & JOHANSON Z., 1998. - Osteolepiforms and the ancestry of tetrapods. *Nature*, 395: 792-794.

AHLBERG P.E. & TREWIN N.H., 1995. - The postcranial skeleton of the Middle Devonian lungfish *Dipterus valenciennesi*. *Trans. R. Soc. Edinburgh: Earth Sci.*, 85: 159-175

ALDINGER H., 1937. - Permische Ganoidfische aus Ostgrönland. *Medd. Grønl.*, 102: 5-392.

ANDREWS S.M. & WESTOLL T.S., 1970. - The postcranial skeleton of rhipidistian fishes excluding *Eusthenopteron*. *Trans. R. Soc. Edinburgh,* 68: 391-489.

ANDREWS M., LONG J., AHLBERG P., BARWICK R. & CAMPBELL K., 2006. - The structure of the sarcopterygian *Onychodus jandemarrai* n. sp. from Gogo, Western Australia: with a functional interpretation of the skeleton. *Earth Environ. Sci. Trans. R. Soc. Edinb.*, 96(3): 197-307.

BARWICK R.E., CAMPBELL K.S. & MARK-KURIK E., 1997. - *Tarachomylax*: a new Early Devonian dipnoan from Severnaya Zemlya, and its place in the evolution of the Dipnoi. *Geobios*, 30(1): 45-73.

BAUDELOT E., 1873. - Observations sur la structure et le développement des nageoires de poissoins osseux. *Arch. Zool. Exp.*, 2: 87-244.

BEMIS W.E., 1984. - Paedomorphosis and the evolution of the Dipnoi. *Paleobiology*, 10(3): 293-307.

BEMIS W.E. & NORTHCUTT R.G., 1992. - Skin and blood vessels of the snout of the Australian lungfish, *Neoceratodus forsteri*, and their significance for interpreting the cosmine of Devonian lungfishes. *Acta Zool.*, 73: 115-139.

BERNACSEK G.M., 1977. - A lungfish cranium from the Middle Devonian of the Yukon Territory, Canada. *Palaeontographica A*, 157: 175-200.

BORGEN U.J., 1989. - Cosmine resorption structures on three osteolepid jaws and their biological significance. *Lethaia*, 22: 413-424.

BORGEN U.J., 1992. - The function of the cosmine pore canal system. *In:* Fossil Fishes as Living Animals (Mark-Kurik E., ed.), pp. 141-150. Academy of Sciences of Estonia, Tallinn, Estonia.

BORGEN U.J. & NAKREM H.A., 2016 - Morphology, phylogeny and taxonomy of osteolepiform fish. *Fossils Strata*, 61: 1-514.

BRIEN P., 1962. - Étude de la formation, de la structure des écailles des dipneustes actuels et de leur comparaison avec les autres types d'écailles des poissons. *Ann. Mus. R. Afr. Cent.*, 108: 53-129.

BYSTROW A.P., 1939. - Zahnstruktur der Crossopterygier. *Acta Zool.,* 20: 283-338.

BYSTROW A.P., 1959. - The microstructure of skeleton elements in some vertebrates from lower Devonian deposits of the USSR. *Acta Zool.*, 40(1): 59-83.

BARWICK R.E. & CAMPBELL K.S.W. 1996. - A Late Devonian dipnoan, *Pillararhynchus*, from Gogo, Western Australia, and its relationships. *Palaeontographica Abteilung A*: 1-42.

CAMPBELL K.S.W. & BARWICK R.E., 1983. - Early evolution of dipnoan dentitions and a new genus *Speonesydrion*. *Mem. Ass. Australas. Palaeontol.*, 1: 17-49.

CAMPBELL K.S.W. & BARWICK R.E., 1988. - *Uranolophus*: a reappraisal of a primitive dipnoan. *Mem. Ass. Australas. Palaeontols.,* 7: 87-144.

CAMPBELL K.S.W. & BARWICK R.E., 1998. - A new tooth-plated dipnoan from the Upper Devonian Gogo Formation and its relationships. *Mem. Queensl. Mus.*, 42: 403-437.

CAMPBELL K., BARWICK R., CHATTERTON B.D.E. & SMITHSON T.R., 2002. - A new Middle Devonian dipnoan from Morocco: structure and histology of the dental plates. *Rec. Aust. Mus.*, 21: 39-61.

CAMPBELL K.S.W., BARWICK R.E. & SENDEN T.J., 2009. - Evolution of dipnoans (lungfish) in the Early Devonian of southeastern Australia. *Alcheringa*, 33(1): 59-78.

CAMPBELL K.S.W., BARWICK R.E. & SENDEN T., 2010. - Perforations and tubules in the snout region of Devonian dipnoans. In Morphology, Phylogeny and Paleobiogeography of Fossil Fishes (Elliott D.K., Malsey J.G., Yu X. & Miao D., eds), pp. 325-361. Verlag Dr Friedrich Pfeil, Germany.

CASTANET J., MEUNIER F., BERGOT C. & FRANÇOIS Y., 1975. - Données préliminaires sur les structures histologiques du squelette de *Latimeria chalumnae*. I – Dents, écailles, rayons de nageoires. Problèmes actuels de Paléontologie. Évolution des Vertébrés, pp. 159-168. Coll. Int. du CNRS, Paris.

CHANG M.M., 1982. - The braincase of *Youngolepis*, a Lower Devonian crossopterygian from Yunnan, southwestern China. Ph.D. dissertation, 113 p. Stockholm University, Stockholm, Sweden.

CHANG M.M. & SMITH M.M., 1992. - Is *Youngolepis* a Porolepiform? *J. Vertebr. Paleontol/,* 12(3): 294-312.

CHANG M.M. & WANG, J.Q., 1995. - A new Emsian dipnorhynchid (Dipnoi) from Guangnan, southeastern Yunnan, China. *Geobios,* 19: 233-239.

CHANG M.M. & YU X., 1981. - A new crossopterygian, *Youngolepis praecursor*, gen. et sp. nov., from Lower Devonian of E. Yunnan, China. *Sci. Sin.*, 24: 89-97.

CHANG M.M. & YU X., 1984. - Structure and phylogenetic significance of *Diabolichthys speratus* gen. et sp. nov., a new dipnoan-like form from the Lower Devonian of Eastem Yunnan, China. *Proc. Linn. Soc. N. S. W*, 107: 171-184.

CHANG M.M. & ZHU M., 1993. - A new Middle Devonian osteolepidid from Quijing, Yunnan. *Mem. Ass. Australas. Palaeontol.,* 15: 183-198.

CHOO B., ZHU M., ZHAO W., JIA L. & ZHU Y.A., 2014. - The largest Silurian vertebrate and its palaeoecological implications. *Sci. Rep.*, 4.

CHOO B., ZHU M., QU Q., YU X., JIA L. & ZHAO W., 2017. - A new osteichthyan from the late Silurian of Yunnan, China. *PloS ONE*, 12(3): e0170929.

CLACK J.A., 2002. - Gaining Ground. The Origin and Evolution of Tetrapods. 369 p. Indiana University Press, Bloomington, USA.

CLÉMENT G., 1999. - The actinistian (Sarcopterygii) *Piveteauia madagascariensis* Lehman from the Lower Triassic of northwestern Madagascar: a redescription on the basis of new material. *J. Vertebr. Paleontol.*, 19(2), 234-242.

CLÉMENT G., 2002. - Large Tristichopteridae (Sarcopterygii, Tetrapodomorpha) from the Late Famennian Evieux Formation of Belgium. *Palaeontology*, 45(3): 577-593.

CLÉMENT G., 2004. - Nouvelles données anatomiques et morphologie générale des "Porolepididae" (Dipnomorpha, Sarcopterygii*). Rev. Paléobiol., Genève,* Vol. Spéc., 9: 193-211.

CLÉMENT G., 2005. - A new coelacanth (Actinistia, Sarcopterygii) from the Jurassic of France, and the question of the closest relative fossil to *Latimeria*. *J. Vertebr. Paleontol*., 25(3): 481-491.

CLEMENT A.M., 2009. - A new genus of lungfish from the Givetian (Middle Devonian) of central Australia. *Acta Palaeontol. Pol*., 54(4): 615-626.

CLÉMENT G. & AHLBERG P.E., 2010. - The endocranial anatomy of the early sarcopterygian *Powichthys* from Spitsbergen, based on CT scanning. *In:* Morphology, Phylogeny and Paleobiogeography of Fossil Fishes (Elliot D.K., Maisey J.G., Yu X. & Miao D., eds) pp. 363-377. Verlag Dr. Friedrich Pfeil, München, Germany.

CLÉMENT G. & JANVIER P., 2004. - *Powichthys spitsbergensis* sp. nov., a new member of the Dipnomorpha (Sarcopterygii, lobe-finned fishes) from the Lower Devonian of Spitsbergen, with remarks on basal dipnomorph anatomy. *Fossils Strata,* 50: 92-112.

CLOUTIER R., 1996a. - The primitive actinistian *Miguashaia bureaui* Schultze (Sarcopterygii). *In:* Devonian Fishes and Plants of Miguasha, Quebec, Canada (Schultze H.P. & Cloutier R., eds), pp. 227-247. Verlag Dr. Friedrich Pfeil, München, Germany.

CLOUTIER R., 1996b. - Dipnoi (Akinetia: Sarcopterygii). *In:* Devonian Fishes and Plants of Miguasha, Quebec, Canada (Schultze H.P. & Cloutier R., eds), pp. 198-152. Verlag Dr. Friedrich Pfeil, München, Germany.

CLOUTIER R., 2010. - The fossil record of fish ontogenies: insights into developmental patterns and processes. *Semin. Cell Dev. Biol*., 21: 400-413.

CLOUTIER R. & AHLBERG P.E., 1996. - Morphology, characters, and the interrelationships of basal sarcopterygians. *In* Interrelationships of Fishes (Stiassny M.L.J., Parenti L.R. & Johnson G.D., (eds), pp. 445-479. Academic Press, San Diego, USA.

CLOUTIER R., PROUST J.N. & TESSIER B., 2011. - The Miguasha Fossil-Fish Lagerstätte: a consequence of the Devonian land-sea interactions. *Palaeobiodiver. Palaeoenviron*., 91(4): 293-323.

COATES M.I., 1996. - The Devonian tetrapod *Acanthostega gunnari* Jarvik: postcranial anatomy, basal tetrapod interrelathionships and patterns of skeletal evolution. *Trans. R. Soc. Edimburg: Earth Sci*., 87: 363-421.

COATES M.I. & FRIEDMAN M., 2010. - *Litoptychus bryanti* and characteristics of stem tetrapod neurocrania. *In:* Morphology, Phylogeny and Paleobiogeography of Fossil Fishes (Elliot D.K., Maisey J.G., Yu X. & Miao D., eds), pp. 389-416. Verlag Dr. Friedrich Pfeil, München, Germany.

CRESSLER W.E., DAESCHLER E.B., SLINGERLAND R. & PETERSON D., 2010. - Terrestrialization in the Late Devonian: a palaeoecological overview of the Red Hill site, Pennsylvania, USA. *In* The Terrestrialization Process: Modelling Complex Interactions at the Biosphere-Geosphere Interface (Vecoli M., Clément G. & Meyer-Berthaud B., eds), pp. 111-128. Geological Society, London, Spec. Publ. 39, London, UK.

DAESCHLER E.B., SHUBIN N.H. & JENKINS F.A. Jr., 2006. - A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. *Nature*, 440: 757-763.

DENISON R.H., 1951. - Late Devonian freshwater fishes from the western United States. *Fieldiana (Geology)*, 11: 221-261.

DENISON R.H., 1968a. - The evolutionary significance of the earliest known lungfish *Uranolophus*. *In:* Current Problems of Lower Vertebrate Phylogeny, Proceedings of the Fourth Nobel Symposium (Ørvig T., ed.), pp. 247-257. Almqvist and Wiksell, Stockholm, Sweden.

DENISON R.H., 1968b. - Early Devonian lungfishes from Wyoming, Utah and Idaho. *Fieldiana (Geology),* 17: 351-413.

DIAS E.V. & RICHTER M., 2002. - On the squamation of *Australerpeton cosgriffi* Barberena, a temnospondyl amphibian from the Upper Permian of Brazil. *An. Acad. Bras. Ciênc.,* 74(3): 477-490.

DONOGHUE P.C.J., 2002. - Evolution of development of the vertebrate dermal and oral skeletons: unraveling concepts, regulatory theories, and homologies. *Paleobiology*, 28(4): 474-507.

DONOGHUE P.C.J., SANSOM I.J. & DOWNS J.P., 2006. - Early evolution of vertebrate skeletal tissues and cellular interactions, and the canalization of skeletal development. *J. Exp. Zool. (Mol. Dev. Evol.)*, 306B: 1-17.

FOREY P.L., 1998. - History of the Coelacanth Fishes. 419 p. Chapman & Hall, London, UK.

FOREY P.L. & YOUNG V.T., 1985. - Acanthodian and coelacanth fish from the Dinantian of Foulden, Berwickshire, Scotland. *Earth Environ. Sci. Trans. R. Soc. Edinburgh*, 76(1): 53-59.

FOREY P., AHLBERG P.E., LUKSEVICS E. & ZUPINS I., 2000. - A new coelacanth from the Middle Devonian of Latvia. *J. Vertebr. Paleontol.,* 20(2): 243-252.

FORSTER-COOPER C., 1937. - VII. – The Middle Devonian Fish Fauna of Achanarras. *Earth Environ. Sci. Trans. R. Soc. Edinburgh*, 59(1): 223-239.

FOX R.C., CAMPBELL K.S.W., BARWICK R.E. & LONG J.A., 1995. - A new osteolepiform fish from the Lower Carboniferous Raymond Formation, Drummond Basin, Queensland. *Mem. Queensl. Mus*., 38: 97-223.

FRANCILLON-VIEILLOT H., BUFFRENIL V. de, CASTANET J., GÉRAUDIE J., MEUNIER F.J., SIRE J.Y., ZYLBERBERG L. & RICQLÈS. A. de, 1990. - Microstructure and mineralization of vertebrate skeletal tissues. *In:* Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends (Carter J.G., ed.), Vol. 1., pp: 471-530. Van Nostrand Reinhold, New York, USA.

FRIEDMAN M., 2007. - *Styloichthys* as the oldest coelacanth: implications for early osteichthyan interrelationships. *J. Syst. Palaeontol*., 5: 289-343.

FRIEDMAN M. & BRAZEAU M.D., 2010. - A reappraisal of the origin and basal radiation of the Osteichthyes. *J. Vertebr. Paleontol.,* 30(1): 36-56.

FRIEND P.F. & MOODY-STUART M., 1973 - Sedimentation of the Wood Bay Formation (Devonian) of Spitsbergen: regional analysis of a late orogenic basin. *Nor. Polarinst. Skr.,* 157: 1-80.

GILES S., COATES M. I., GARWOOD R.J., BRAZEAU M.D., ATWOOD R., JOHANSON Z., FRIEDMAN M. & RUTA M., 2015a. - Endoskeletal structure in *Cheirolepis* (Osteichthyes, Actinopterygii), an early ray-finned fish. *Palaeontology,* 58*:* 849-870.

GILES S., DARRAS L., CLÉMENT G., BLIECK A. & FRIEDMAN M., 2015b. - An exceptionally preserved Late Devonian actinopterygian provides a new model for primitive cranial anatomy in ray-finned fishes. *Proc. R. Soc. B*, 282(1816): 20151485.

GOODRICH E.S., 1904. - On the dermal fin-rays of fishes – living and extinct. *Quart. J. Microsc. Sci.e*, 47: 465-522.

GOODRICH E.S., 1907. - On the scales of fish living and extinct, and their importance in classification. *Proc. Zool. Soc. Lond*., 47(4): 751-774.

GROGAN E.D. & LUND R., 2015. - Two new Actinopterygii (Vertebrata, Osteichthyes) with cosmine from the Bear Gulch Limestone (Heath Fm., Serpukhovian, Mississippian) of Montana USA. *Proc. Acad. Nat. Sci.s Philad.*, 164(1): 111-132.

GROSS W., 1933. - Die unterdevonischen Fische und Gigantostraken von Overath. *Abh. Preuss. Geol. Landesanstalt,* 145: 41-77.

GROSS W., 1956. - Über Crossopterygier und Dipnoer aus dem baltischen Oberdevon im Zusammenhang einer vergleichenden Untersuchung des Porenkanalsystems paläozoischer Agnathen und Fische. *K. Sven. Vetenskapsakad. Handl., 4^{e} Ser.*, 5(6): 1-140.

GROSS W., 1966. - Kleine Schuppenkunde. *Neues Jahrb. Geol. Paläontol., Abh.,* 125: 29-48.

HOLLAND T., 2009. - *Owensia chooi*: a new tetrapodomorph fish from the Middle Devonian of the South Blue Range, Victoria, Australia. *Alcheringa*, 33(4): 339-353.

JANVIER P., 1996. - Early Vertebrates. Oxford Monographs on Geology and Geophysics, 33. 393 p. Clarendon Press, Oxford, UK.

JANVIER P. & PHUONG T.H., 1999 - Les vertébrés (Placodermi, Galeaspida) du Dévonien inférieur de la coupe de Lung Cô-Mia Lé, province de Hà Giang, Viêt Nam, avec des données complémentaires sur les gisements à vertébrés du Dévonien du Bac Bo oriental. *Geodiversitas,* 21(1): 33–67.

JANVIER P., CLÉMENT G. & CLOUTIER R., 2007. - A primitive megalichthyid fish (Sarcopterygii, Tetrapodomorpha) from the Upper Devonian of Turkey and its biogeographical implications. *Geodiversitas*, 29: 249-268.

JARVIK E., 1948. - On the morphology and taxonomy of the Middle Devonian osteolepidid fishes of Scotland. *K. Sven. Vetenskapsakad. Handl.,* 25: 1-301.

JARVIK E., 1950. - On some osteolepiform crossopterygians from the upper Old Red Sandstone of Scotland. *K. Sven. Vetenskapsakad. Handl.,* 2(4): 1-35.

JARVIK E., 1952. - On the fish-like tail in the ichthyostegid stegocephalians with descriptions of a new stegocephalian and a new crossopterygian from the Upper Devonian of East Greenland. *Medd. Grønland*, 114(12): 1-90.

JARVIK E., 1959. - Dermal fin rays and Holmgren's principle of delamination. *K. Sven. Vetenskapsakad. Handl.*, 6(1): 1-51.

JARVIK E., 1972. - Middle and Upper Devonian Porolepiformes from East Greenland with special reference to *Glyptolepis groenlandica* n. sp., and a discussion on the structure of the head in the Porolepiformes. *Medd. Grønl.*, 187(2): 1-307.

JARVIK E., 1980. - Basic Structure and Evolution of Vertebrates, Vol. 1. 575 p. Academic Press, London, UK.

JARVIK E., 1985. - Devonian osteolepiform fishes from East Greenland. *Medd. Grønland, Geosci.,* 13: 1-52.

JARVIK E., 1996. - The Devonian tetrapod *Ichthyostega*. *Fossils Strata*, 40: 1-206.

JESSEN H.L., 1966. - Die Crossopterygier des Oberen Plattenkalkes (Devon) der Bergisch Gladbach-Paffrather Mulde (Rheinischer Schiefergebirge) unter Berücksichtigung von amerikanischem und europaischem *Onychodus* Material. *Ark. Zool.,* 18(2): 305-389.

JESSEN H., 1967. - The position of the Struniiformes Strunius and Onychodus among the crossopterygians. *Coll. Int. CNRS*, 163: 173-180.

JESSEN H.L., 1973. - Weitere Fischreste aus dem Oberen Plattenkalk der Bergisch Gladbach Paffrather Mulde (Oberdevon Rheinischer Schiefergebirge). *Palaeontogr. Abt. (A)*, 143: 159-187.

JESSEN H.L., 1975. - A new choanate fish, *Powichthys thorsteinssoni* n. g., n. sp., from the early Lower Devonian of the Canadian Arctic archipelago. *In:* Problèmes Actuels de Paléontologie Evolution des Vertébrés (Lehman J.P., ed.), pp. 213-222. Colloques Internationaux du Centre National de la Recherche Scientifique, 218. Editions du CNRS, Paris, France.

JOHANSON Z. & AHLBERG P.E. 1998. - A complete primitive rhizodont from Australia. *Nature*, 394: 569-572.

JOHANSON Z. & AHLBERG P.E., 2001. - Devonian rhizodontids and tristichopterids (Sarcopterygii; Tetrapodomorpha) from East Gondwana. *Trans. R. Soc. Edinburgh: Earth Sci.,* 92: 43-37.

JOHANSON Z., LONG J.A., TALENT J.A., JANVIER P. & WARREN J.W., 2007. - New onychondontiform (Osteichthyes; sarcopterygii) from the Lower Devonian of Victoria, Australia. *J. Paleontol.*, 81(5): 1031-1043.

KERR T., 1955. - The scales of modern lungfish. *Proc. Zool. Soc. Lond.,* 125(2): 335-345.

KRUPINA N.I., REISZ R.R., & SCOTT D., 2001. - The skull and tooth system of *Orlovichthys limnatis*, a Late Devonian dipnoan from Russia. *Canadian Journal of Earth Sciences,* 38: 1301–1311.

LEBEDEV O.A., 1983 - A new crossopterygian fish from the Central Devonian Region. *Palaeontol. J.*, 4: 68-75. [In Russian].

LEBEDEV O., 1995a. - Morphology of a new osteolepidid fish from Russia. *Bull. Mus. Natl. Hist. Nat., Paris*, 4^{e} sér., Sect. C, 17(4): 287-341.

LEBEDEV O., 1995b. - Middle Famennian (Upper Devonian) chondrichthyans and sarcopterygians from Oryol region, Central Russia. *Geobios*, 19: 361-368.

LEBEDEV O. & COATES M.I., 1995. - The postcranial skeleton of the Devonian tetrapod *Tulerpeton curtum* Lebedev. *Zool. J. Linn. Soc.,* 11: 307-348.

LEHMAN J.P., 1959. - Les Dipneustes du Devonian supérieur du Groenland. *Medd. Grønl.*, 160: 1-58.

LEHMANN W.M. & WESTOLL T.S., 1952. - A primitive dipnoan fish from the Lower Devonian of Germany. *Proc. R. Soc. Lond. B,* 140: 403–421.

LONG J.A., 1985. - The structure and relationships of a new osteolepiform fish from the Late Devonian of Victoria, Australia. *Alcheringa,* 9: 1-22.

LONG J.A., 1987. - An unusual osteolepiform fish from the Late Devonian of Victoria, Australia. *Palaeontology,* 30: 839-852.

LONG J.A. 1992. - *Gogodipterus paddyensis* (Miles), gen. nov., a new chirodipterid lungfish from the late Devonian Gogo Formation, Western Australia. *The Beagle,* 9: 11-20.

LONG J.A., 1999. - A new genus of fossil coelacanth (Osteichthyes: Coelacanthiformes) from the Middle Devonian of southeastern Australia. *Rec. West. Aust. Mus.,* Suppl., 57: 37-53.

LONG J.A., 2010. - New holodontid lungfishes from the Upper Devonian Gogo Formation of Western Australia. *In:* Morphology, Phylogeny and Paleobiogeography of Fossil Fishes (Elliot D.K., Maisey J.G., Yu X. & Miao D., eds), pp. 275-298. Verlag Dr. Friedrich Pfeil, München, Germany.

LONG J.A. & TRINAJSTIC K., 2010 - The Late Devonian Gogo Formation Lägerstatte of Western Australia: exceptional early vertebrate preservation and diversity. *Ann. Rev. Earth Planet. Sci.*, 38: 255-279.

LONG J.A., BARWICK R.E. & CAMPBELL K.S.W., 1997. - Osteology and functional morphology of the osteolepiform fish *Gogonasus andrewsae* Long, 1985, from the Upper Devonian Gogo Formation, Western Australia. *Rec. West. Aust. Mus.*, Suppl., 53: 1-89.

LONG J. A., CAMPBELL K. S. W. & BARWICK R. E., 1994. - A new dipnoan genus, Ichnomylax, from the Lower Devonian of Victoria, Australia. *J. Vertebr. Paleontol.*, 14(1): 127-131.

LONG J.A., LARGE R.R., LEE M.S., BENTON M.J., DANYUSHEVSKY L.V., CHIAPPE L.M., HALPIN J.A., CANTRILLH D. & LOTTERMOSERC B., 2016. - Severe selenium depletion in the Phanerozoic oceans as a factor in three global mass extinction events. *Gondwana Res.*, 36: 209-218.

LU J. & ZHU M., 2008. - An Early Devonian (Pragian) sarcopterygian from Zhaotong, Yunnan, China. *Vertebr. Palasiat.*, 46: 161-170.

LU J. & ZHU M., 2010. - An onychodont fish (Osteichthyes, Sarcopterygii) from the Early Devonian of China, and the evolution of the Onychodontiformes. *Proc. R. Soc. B,* 277: 293-299.

LU J., ZHU M., LONG J.A., ZHAO W., SENDEN T.J., JIA L. & QIAO T., 2012. - The earliest known stem-tetrapod from the Lower Devonian of China. *Nat. Commun.,* 3: 1160.

LU J., GILES S., FRIEDMAN M., DEN BLAAUWEEN J.L. & ZHU M., 2016a. - The oldest actinopterygian highlights the cryptic early history of the hyperdiverse ray-finned fishes. *Curr. Biol.*, 26 (12): 1602-1608.

LU J., ZHU M., AHLBERG P.E., QIAO T., ZHU Y.A., ZHAO W. & JIA L., 2016b. - A Devonian predatory fish provides insights into the early evolution of modern sarcopterygians. *Sci. Adv.*, 2(6): p.e1600154.

LU J., GILES S., FRIEDMAN M. & ZHU M., 2017. - A new stem sarcopterygian illuminates patterns of character evolution in early bony fishes. *Nat. Commun.*, 8: 1932.

MEINKE D.K., 1982. - A light and scanning electron microscope study on the dermal skeleton of *Spermatodus pustulosus* (Pisces: Coelacanthini) and the evolution of the dermal skeleton in coelacanths. *J. Paleontol.*, 56: 620- 630.

MEINKE D.K., 1984. - A review of cosmine: its structure, development, and relationships to the other forms of the dermal skeleton in osteichthyans. *J. Vertebr. Paleontol.*, 4: 457-470.

MEUNIER F.J., 1980. - Les relations isopedine - tissu osseux dans le post-temporal et les écailles de la ligne latérale de *Latimeria chalumnae* (Smith). *Zool. Scr.*, 9(1-4): 307-317.

MEUNIER F.J., 1984. - Spatial organization and mineralization of the basal plate of elasmoid scales in osteichthyans. *Am. Zool.*, 2 (4): 953-964.

MEUNIER F.J., 2011. - The Osteichtyes, from the Paleozoic to the extant time, through histology and palaeohistology of bony tissues. *C. R. Palevol*, 1 (5): 347-355.

MEUNIER F.J. & GAYET M., 1992. - Remaniement de la ganoïne chez un sémionotidae nouveau du Crétacé Supérieur de Bolivie: intérêt paleobiologique. *Geobios,* 25(6): 767-774.

MILES R.S., 1977. - Dipnoan (lungfish) skulls and the relationships of the group: A study based on new species from the Devonian of Australia. *Zool. J. Linn. Soc.*, 61: 1-328.

MONDÉJAR-FERNÁNDEZ J. & CLÉMENT G., 2012. - Squamation and scale microstructure evolution in the Porolepiformes (Sarcopterygii, Dipnomorpha) based on *Heimenia ensis* from the Devonian of Spitsbergen. *J. Vertebr. Paleontol.,* 32(2): 267-284.

MONDÉJAR-FERNÁNDEZ J., CLÉMENT G. & SANCHEZ S., 2014. - New insights into the scales of the Devonian tetrapod *Tulerpeton curtum* Lebedev, 1984. *J. Vertebr. Paleontol.*, 34(6): 1454-1459.

MOY-THOMAS J.A., 1971. - Palaeozoic Fishes. 2nd Edit., 260 p. Saunders, Philadelphia.

NEWBERRY J.S., 1889. - The Paleozoic Fishes of North America. *Monogr. U. S. Geol. Surv.*, Vol. 16, 466 p.

NEWMAN M.J. & DEN BLAAUWEN J.L., 2007. - A new dipnoan fish from the Middle Devonian (Eifelian) of Scotland. *Palaeontology*, 50(6): 1403-1419.

NORTHCUTT R.G. & GANS C., 1983. - The genesis of neural crest and epidermal placodes: a reinterpretation of vertebrate origins. *Quart. Rev. Biol.*, 58(1): 1-28.

OBRUCHEV D.V., 1941. - Devonian fishes of the Minusinsk Area. *Tr. Paleontol. Inst.*, 8(4): 23-48 [In Russian].

OBRUCHEV O.P., 1955. - Upper Devonian fishes from Central Kazakhstan. *Sov. Geol.*, 45: 84-93 [In Russian].

ØRVIG T., 1957. - Remarks on the vertebrate fauna of the lower Upper Devonian of Escuminac Bay, P.Q. Canada, with special reference to the porolepiform crossopterygians. *Ark. Zool.,* 10 (6): 367-426.

ØRVIG T., 1968. - The dermal skeleton: General considerations. *In:* Current Problems of Lower Vertebrate Phylogeny, Proceedings of the Fourth Nobel Symposium (Ørvig T., ed.), pp. 374-397. Almquist & Wiksell, Stockholm, Sweden.

ØRVIG T., 1969a. - Cosmine and cosmine growth. *Lethaia*, 2 (4): 241-260.

ØRVIG T., 1969b. - Vertebrates from the Wood Bay Group and the position of the Emsian-Eiffelian boundary in the Devonian of Vestspitsbergen. *Lethaia*, 2(4): 273-328.

OTTO M., 2007. - *Durialepis edentatus* n. gen., n. sp., ein neuer Rhipidistier (Osteichthyes, Sarcopterygii) aus dem Unter-Devon des Rheinischen Schiefergebirges. *Geol. Palaeontol.*, 41: 3-25.

OTTO M. & BARDENHEUER P., 1996. - Lungfish with dipterid tooth-plates in the Lower Devonian of Central Europe. *Modern Geol.*, 20: 341-350.

PEARSON D.M., 1982. - Primitive bony fishes, with especial reference to *Cheirolepis* and palaeonisciform actinopterygians. *Zool. J. Linn. Soc.,* 74: 35-67.

PEARSON D.M. & WESTOLL T.S., 1979. - The Devonian actinopterygian *Cheirolepis* Agassiz. *Earth Environ. Sci. Trans. R. Soc. Edinburgh*, 70(13-14): 337-399.

QIAO T. & ZHU M., 2009. - A new tooth-plated lungfish from the Middle Devonian of Yunnan, China, and its phylogenetic relationships. *Acta Zool.*, 9 (s1): 236-252.

QU Q.M., ZHU M. & WANG W., 2013a. - Scales and dermal skeletal histology of an early bony fish *Psarolepis romeri* and their bearing on the evolution of rhombic scales and hard tissues. *PLoS ONE*, 8: e61485.

QU Q.M., SANCHEZ S., BLOM H., TAFFOREAU P. & AHLBERG P.E., 2013b. - Scales and tooth whorls of ancient fishes challenge distinction between external and oral 'teeth'. *PLoS ONE,* 8: e71890.

QU Q.M., HAITINA T., ZHU M. & AHLBERG P.E., 2015. New genomic and fossil data illuminate the origin of enamel. *Nature,* 526: 108-111.

QU Q., SANCHEZ S., ZHU M., BLOM H. & AHLBERG P., 2016. - The origin of novel features by changes in developmental mechanisms: ontogeny and three-dimensional microanatomy of polyodontode scales of two early osteichthyans. *Biol. Rev.*, 92(2): 1189-1212.

REIF W.E., 1982. - Evolution of dermal skeleton and dentition in vertebrates. *In*: Evolutionary Biology (Hecht M.K., Wallace B. & Prance G.T., eds), pp. 287-368. Springer, Boston, US.

RICHTER M. & SMITH M., 1995. - A microstructural study of the ganoine tissue of selected lower vertebrates. *Zool. J. Linn. Soc.* 114: 173-2121.

ROSEN D.E., FOREY P.L. GARDINER B.G. & PATTERSON C., 1981. - Lungfishes, tetrapods, paleontology, and plesiomorphy. *Bull. Am. Mus. Nat. Hist.*, 167(4): 159-276.

ROUX G.H., 1942. - The microscopic anatomy of the *Latimeria* scale. *S. Afr. J. Med. Sci. 7* (Bioi. Suppl.): l-18.

SCHAEFFER B., 1941. - A revision of Coelacanthus newarki and notes on the evolution of girdles and basal plates of the medial fins in the Coelacanthini. *Am. Mus. Nat. Hist. Novit.*, 1110: 1-17.

SCHAEFFER B., 1952. - The Triassic coelacanth *Diplurus*, with observations on the evolution of the Coelacanthini. *Bull. Am. Mus. Nat. Hist.*, 99: 25-78.

SCHAEFFER B., 1962. - A coelacanth fish from the Upper Devonian of Ohio. *Sci. Publ. Cleveland Mus. Nat. Hist.*, 1: 1-14.

SCHAEFFER B., 1977. - The dermal skeleton in fishes. *In:* Problems in Vertebrate Evolution (Andrews S.M., Miles R.S. & Walker A.D., eds.), pp. 25-51. Linnean Society Series 4. Academic Press, London, UK.

SCHULTZE H.P., 1969a. - *Griphognathus* Gross, ein langschnauziger Dipnoer aus dem Oberdevon von Bergisch-Gladbach (Rheinisches Schiefergebirge) und von Lettland. *Geol. Paleontol.*, 3: 21-79.

SCHULTZE H.P., 1969b. - Die Faltenzähne der Rhipidistiden Crossopterygier, der Tetrapoden und der Actinopterygier-gattung *Lepisosteus*. *Palaeontogr. Ital.*, 65: 63-136.

SCHULTZE H.P., 1992. - A new long-headed dipnoan (Osteichthyes) from the Middle Devonian of Iowa, USA. *J. Vertebr. Paleontol.*, 1 (1): 42-58.

SCHULTZE H.P., 1996. - The elpistostegid fish *Elpistostege*, the closest the Miguasha fauna comes to a tetrapod. *In:* Devonian Fishes and Plants of Miguasha, Quebec, Canada (Schultze H.P. & Cloutier R., eds), pp. 316-327. Verlag Dr. Friedrich Pfeil, München, Germany.

SCHULTZE H.P., 2000. - A porolepiform rhipidistian from the Lower Devonian of the Canadian Arctic. *Fossil Rec.*, 3: 99-109.

SCHULTZE H.P., 2001. - *Melanognathus,* a primitive dipnoan from the Lower Devonian of the Canadian Arctic and the interrelationships of Devonian dipnoans. *J. Vertebr. Paleontol.*, 21(4): 781-794.

SCHULTZE H.P., 2015. - Scales, enamel, cosmine, ganoine, and early osteichthyans. *C. R. Palevol*, 15(1-2): 83-102.

SCHULTZE H.P. & CHORN J., 1997. - The Permo-Carboniferous genus Sagenodus and the beginning of modern lungfish. *Contrib. Zool.*, 67(1): 9-70.

SCHULTZE H.P. & CHORN J., 1998. - Sarcopterygian and other fishes from the marine Upper Devonian of Colorado, U.S.A. *Mitt. Mus. Naturk. Berlin, Geowiss. Reihe,* 1: 53-72.

SCHULTZE H.P. & HEIDTKE U., 1986. - Rhizodopside Rhipidistia (Pisces) aus dem Perm der Pfalz (W-Deutschland). *Neues Jahrb. Geol. Paläontol., Monatsh.,* 4: 215-228.

SIRE J.Y., DONOGHUE P.C. & VICKARYOUS M.K., 2009. - Origin and evolution of the integumentary skeleton in non-tetrapod vertebrates. *J. Anat.,* 214: 409-440.

SMITH M.M., 1977. - The microstructure of the dentition and dermal ornament of three dipnoans from the Devonian of Western Australia: a contribution towards dipnoan interrelations and morphogenesis, growth, and adaptation of the skeletal tissues. *Philos. Trans. R. Soc. Lond. (B),* 281: 29-72.

SMITH M.M., 1979. - Scanning electron microscopy of odontodes in the scales of a coelacanth embryo, *Latimeria chalumnae* Smith. *Arch. Oral Biol.*, 24(2): 179-183.

SMITH M.M., HOBDELL M.H. & MILLER W.A., 1972. - The structure of the scales of *Latimeria chalumnae*. *J. Zool.*, 167: 501-509.

SNITTING D., 2008. - A redescription of the anatomy of the Late Devonian *Spodichthys buetleri* Jarvik, 1985 (Sarcopterygii, Tetrapodomorpha) from East Greenland. *J. Vertebr. Paleontol.*, 28(3): 637-655.

STENSIÖ E.A., 1937. - On the Devonian coelacanthids of Germany with special reference to the dermal skeleton. *K. Sven. Vetenskapsakad. Handl.,* Ser. 3, 16: 1-56.

THOMSON K.S., 1967. - A new genus and species of marine dipnoan fish from the Upper Devonian of Canada. *Postilla*, 106: 1-6.

THOMSON K.S., 1968. - A new Devonian fish (Crossopterygii: Rhipidistia) considered in relation to the origin of the Amphibia. *Postilia*, 124: 1-13.

THOMSON K.S., 1972. - New evidence of the evolution of the paired fins of Rhipidistia and the origin of the tetrapod limb, with description of a new genus of Osteolepididae. *Postilla,* 157: 1-7.

THOMSON K.S., 1973. - Observations on a new rhipidistian fish from the Upper Devonian of Australia. *Palaeontographica* A, 143: 209-220.

THOMSON K.S., 1975. - On the biology of cosmine. *Bull. Peabody Mus. Nat. Hist.,* 40: 1-57.

THOMSON K.S., 1977. - On the individual history of cosmine and a possible electroreceptive function of the pore-canal system in fossil fishes. *In:* Problems in Vertebrate Evolution (Andrews S.M., Miles R.S. & Walker A.D., eds), pp. 247-270. Linnean Society Series 4. Academic Press, London, UK.

THOMSON K.S. & CAMPBELL K.S.W., 1971. - The structure and relationships of the primitive dipnoan lungfish *Dipnorhynchus sussmilchi* (Etheridge). *Bull. Peabody Mus. Nat. Hist.,* 38: 1-109.

VOROBYEVA E.I., 1959. - A new crossopterygian fish genus *Platycephalichthys* from the Upper Devonian of the Lovat River. *Paleontol. Z.,* 3: 95-106. [in Russian]

VOROBYEVA E.I., 1962. - Rhizodont crossopterygians fishes from the main Devonian field of the USSR. *Tr. Paleontol. Int.,* 94: 1-108. [in Russian]

VOROBYEVA E.I., 1977. - Morphology and nature of evolution of crossopterygian fishes. *Tr. Paleontol. Inst. Akad. Nauk SSSR,* 163: 1-239. [In Russian]

VOROBYEVA E.I. & LYARSKAYA L.A., 1968. - Crossopterygian and dipnoan remains from the Amata beds of Latvia and their burial. *In:* Ocherki po Filogellii i sistematike Iskopaemykh ryb i bezche/illstnykh (Obruchev D.V., ed.), pp. 71-86. Moscow, SSSR. [In Russian]

WANG S., DRAPALA V., BARWICK R.E. & CAMPBELL K.S.W., 1993. - The dipnoan species, *Sorbitorhynchus deleaskitus*, from the Lower Devonian of Guangxi, China. *Philos. Trans. R. Soc. Lond.*, B 340: 1-24.

WESTOLL T.S., 1936. - On the structures of the dermal ethmoid shield of *Osteolepis*. *Geol. Mag.*, 73(4): 157-171.

WESTOLL T.S., 1938. - Ancestry of the tetrapods. *Nature*, 141(3559): 127-128.

WESTOLL T.S. & ROMER A.S., 1939. - On *Spermatodus pustulosus* Cope, a coelacanth from the "Permian" of Texas. *Am. Mus. Novit.*, 1017: 1-23.

WHITE E.I., 1965. - The head of *Dipterus valenciennesi* Sedgwick and Murchison. *Bull. Br. Mus. Nat. Hist. (Geol.),* 11: 1-45.

WILLIAMSON W.C., 1849. - On the microscopic structure of the scales and dermal teeth of some ganoid and placoid Fish. *Philos. Trans. R. Soc. Lond*, 139: 435-475.

WITZMANN F., 2011. - Morphological and histological changes of dermal scales during the fish-to-tetrapod transition. *Acta Zool.*, 92(3): 281-302.

WITZMANN F. & SCHOCH R. R., 2012. - A megalichthyid sarcopterygian fish from the Lower Permian (Autunian) of the Saar-Nahe Basin, Germany. *Geobios*, 45(2): 241-248.

WITZMANN F., SCHOLZ H., MUELLER J. & KARDJILOV N., 2010. - Sculpture and vascularization of dermal bones, and the implications for the physiology of basal tetrapods. *Zool. J. Linn. Soc.*, 160(2): 302-340.

WOROBJEWA E.I., 1975. - The Osteolepidid crossopterygia from Ketleri Suite of Latvia. *Fauna Stratigr. Paleozoya Mezozoya Pribaltiki Beloruss.*: 233-237 [In Russian].

XUN Z., ALLEN M.B, WHITMAN A.G. & PRICE S.P., 1996 - Rift-related Devonian sedimentation and basin development in South China. *J. Southeast Asian Earth Sci.*, 14(1/2): 37-52.

YOUNG G.C. & SCHULTZE H.P., 2005. - New osteichthyans (bony fishes) from the Devonian of Central Australia. *Mitt. Mus. Naturk. Berlin, Geowiss. Reihe,* 8: 13-35.

YOUNG G.C., LONG J.A. & RITCHIE A., 1992. - Crossopterygian fishes from the Devonian of Antarctica: Systematics, relationships and biogeographic significance. *Rec. West. Aust. Mus.,* Suppl., 14: 1-77.

YU X., 1998. - A new porolepiform-like fish, *Psarolepis romeri*, gen. et sp. nov. (Sarcopterygii, Osteichthyes) from the Lower Devonian of Yunnan, China. *J. Vertebr. Paleontol.,* 18(2): 261-274.

ZHU M. & AHLBERG P.E., 2004. - The origin of the internal nostril of tetrapods. *Nature*, 432: 94-96.

ZHU M. & YU X., 2002. - A primitive fish close to the common ancestor of tetrapods and lungfish. *Nature*, 418: 767-770.

ZHU M. & ZHAO W., 2005. - An onychodont-like sarcopterygian fish from the Middle Devonian of Yunnan, southwestern China. *J. Vertebr. Paleontol.*, 25(3, Suppl.): 134 A.

ZHU M., YU X. & JANVIER P., 1999. - A primitive fossil fish sheds light on the origin of bony fishes. *Nature,* 397: 607-610.

ZHU M., YU X. & AHLBERG P.E., 2001. - A primitive sarcopterygian fish with an eyestalk. *Nature*, 410: 81-84.

ZHU M., YU X., WANG W., ZHAO W. & JIA L., 2006. - A primitive fish provides key characters bearing on deep osteichthyan phylogeny. *Nature*, 441: 77-80.

ZHU M., ZHAO W., JIA L., LU J., QIAO T. & QU Q., 2009. - The oldest articulated osteichthyan reveals mosaic gnathostome characters. *Nature,* 458: 469-474.

ZHU M., WANG W. & YU X., 2010. - *Meemannia eos*, a basal sarcopterygian fish from the Lower Devonian of China – expanded description and significance. *In:* Morphology, Phylogeny and Paleobiogeography of Fossil Fishes (Elliot D.K., Maisey J.G., Yu X.& Miao D., eds), pp. 199-214. Verlag Dr. Friedrich Pfeil, München, Germany.

ZHU M., YU X., LU J., QIAO T., ZHAO W. & JIA L., 2012. - Earliest known coelacanth skull extends the range of anatomically modern coelacanths to the Early Devonian. *Nat. Commun.*, 3: 772.

ZHU M., AHLBERG P.E., ZHAO W.J. & JIA L.T., 2017. - A Devonian tetrapod-like fish reveals substantial parallelism in stem tetrapod evolution. *Nat. Ecol. Evol.*, 1(10): 1470.

ZYLBERBERG L., MEUNIER J.F. & LAURIN M., 2010. - A microanatomical and histological study of the postcranial dermal skeleton in the Devonian sarcopterygian *Eusthenopteron foordi*. *Acta Palaeont. Pol.,* 55(3): 459-470.

ZYLBERBERG L., MEUNIER J.F. & LAURIN M., 2015. - A microanatomical and histological study of the postcranial dermal skeleton of the Devonian actinopterygian *Cheirolepis canadensis*. *Acta Palaeontol. Pol.,* 61(2): 363-376.